A TAXONOMIC STUDY OF THE SAURITUS GROUP OF THE GARTERSNAKES, GENUS *THAMNOPHIS* FITZINGER

By

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INTRODUCTION

Over half a century has elapsed since Ruthven (1908) produced his classic monograph of the gartersnake genus Thamnophis, a monumental work which has served as a model for subsequent studies of geographic variation in ophidians and for taxonomic monographs generally. In that study he arranged the 12 species of Thamnophis then recognized into two primary phylogenetic divisions, each of which contained two species groups which he named for the principal species in each. Thus, his Division I comprised the Radix Group and the Sauritus Group and his Division II the Elegans Group and the Sirtalis Group.

In the course of his revision, Ruthven examined approximately 3000 specimens, a number which, while impressive at first glance, and for that time, is not adequate for detailed variational studies when reduced by dividing it among 12 separate species. This is particularly true when one considers that there actually are about two dozen species of Thamnophis, half of which were not recognized by Ruthven although he apparently had specimens of all but five or six. As additional material accumulated in American museums during the first half of the 20th century, more refined analyses of geographic variation became possible

for many species (Fitch, 1940; Hittleman, 1949; A. E. Smith, 1949; and Milstead, 1953, to mention only the most comprehensive studies). For some unknown reason, the sauritus group has been overlooked in this recent flurry of activity by students of gartersnake variation, except for a few brief and scattered notes buried in papers on other subjects. This general lack of interest in the ribbon-snakes is especially surprising when one considers the extensive geographic range of the group (Nova Scotia to the Great Plains to Costa Rica) and the large amount of material available for study (more than 2400 specimens), two facts which would appear to indicate that the sauritus group would be a good subject for a detailed study of variation, both geographic and individual.

The purpose of this investigation is twofold: to provide an adequate definition of the sauritus group with an eye to using it as a model on which to base comparative studies of all members of the genus Thamnophis (this seems especially appropriate inasmuch as T. sauritus is the type species) and to analyse individual and geographic variation in each of the two species belonging to the group.

MATERIALS AND METHODS

Owing to limitations of time and to other practical considerations, no attempt was made to examine every specimen of Thamnophis sauritus and T. proximus present in North American collections. More than 2400 specimens from all parts of the ranges of both species were studied. This number is sufficient, I believe, to delimit adequately the variation occurring in this group of snakes.

In addition to the preserved material, I have been fortunate in having live ribbonsnakes from many parts of the United States and Mexico available for examination, including living representatives of all of the subspecies recognized in this study. Without these animals, several distinctive and diagnostic color-pattern characters would have gone unnoticed. A small number of articulated and disarticulated skeletons were prepared for comparative purposes, and the left maxilla was removed from a number of the preserved specimens for the purpose of making tooth counts. Sex was determined by dissection, except for those males which had the hemipenes everted.

The following measurements of cephalic scales were made: parietal length, frontal length and width, muzzle length, internasal-rostral suture length, and nasal-rostral

suture length. Muzzle length, as used herein, equals the combined length of a prefrontal and the adjacent internasal when measured along the mid-dorsal suture. These measurements were used to obtain the following ratios: frontal length/parietal length; frontal width/frontal length; muzzle length/frontal length; internasal-rostral contact/nasal-rostral contact. Measurements were also made of head length, body length (including the head), and tail length. Head length/body length and tail length/total length ratios were calculated. Many specimens lack tails or are badly distorted; hence the number for which tail length/total length values could be obtained is small. A few of the ratios (frontal length/parietal length and frontal width/frontal length) showed no significant variation and will not be discussed further.

Standard counts were made of such meristic characters as number of supra- and infralabials, pre- and postoculars, temporals, intergenials, ventrals, and subcaudals, as well as of any anomalies occurring in these characters. The number of dorsal scale rows was determined at three points on the body: one head length behind the head, midbody, and above the last ventral scute. The point of dorsal scale row reduction on the body was determined for a small number of specimens, and caudodorsal reduction in a few individuals.

The number of teeth on each of the dentigerous bones was noted (counts were made only on the left side in any

one individual), empty sockets being included in the total count.

Inasmuch as certain elements of pattern vary significantly in the mauritus Group, the condition of a number of these elements was observed in each specimen. These included relative size and shape of the light-colored parietal spots, extent of the light spot on the postoculars, presence or absence of a black postorbital vitta, width of the vertebral stripe, presence or absence of a black paravertebral stripe, width of the light lateral stripe, degree of spotting between the vertebral and lateral stripes, and width of the dark ventrolateral stripe occupying the lateral margin of the ventral scutes on each side.

Color notes on living specimens were recorded. In this regard consistent attention was given the labials, vertebral and lateral stripes, the dorsum, and the venter. In most cases these evaluations were subjective, but, with only two exceptions, at least one specimen of each geographic race was compared with a color atlas (Maerz and Paul, 1950).

THE SAURITUS GROUP

Introduction

It has recently been shown that T. proximus, long thought to be a subspecies of sauritus, is a valid species (Rossman, MS). The sauritus group, which is now considered to be composed of two closely related species, T. sauritus (Linnaeus) and T. septentrionalis (Say), has long been recognized as being more or less distinct from the other gartersnake species. Holbrook (1842) places the species sauritus (including, but not recognizing, proximus) in Leptophis, a genus of slender, semiarboreal colubrids, but he does not include the other gartersnakes. Fitzinger (1843) erects a new genus, Thamnophis, solely to accommodate the ribbonsnake, although all gartersnakes eventually have been placed in this genus by later authors. Even as late as 1893, Duméril and Bocourt include only sauritus in Thamnophis, the other species being placed in Eutaenia. Ruthven (1908) does not place sauritus in a separate genus, but acknowledges its distinctive nature by making it the only species to constitute an entire species group in his phylogenetic scheme.

Definition of the sauritus Group

These are snakes of the genus Thamnophis possessing a small nasoparietal which extends to the seventh or eighth subcaudal in the inverted position. The number of maxillary teeth ranges from 27 to 34 (mode 30). The basal portion of the tongue is red, the forked tips black. The tail is long, usually constituting 27 percent or more of the total length in adults. The maximum number of dorsal scale rows rarely exceeds 19. The ventrals range from 141 to 181 (both extremes in T. proximus), the subcaudals from 52 (T. proximus) to 136 (T. sauritus). In both species the males have a slightly greater number than the females. The lateral stripe is usually confined to dorsal scale rows 3 and 4. The supralabials always lack vertical black bars.

General Morphology

Form and Proportions

Both species are relatively slender, long-tailed snakes when compared with other members of the genus. Thamnophis proximus may exceed 1250 mm. in total length, being equaled among the garternakes by Thamnophis sirtalis and surpassed only by Thamnophis elegans vagrans. T. sauritus is smaller; the largest adult examined measures only slightly over one meter. The relatively narrow head makes up 3.7 to 4.6 (mean 4.1) percent of the body length in adults. The muzzle is narrow, the internasal-rostral contact/nasal-rostral contact ratio exceeding 1.00 in only

one of 29 adults examined for this character (mean 3.82). This narrowness of muzzle apparently reflects the semi-aquatic habits of these two species (Fitch, 1940; Malnate, 1950).

The tail is longer than in any other species of Thamnophis and constitutes 25.8 to 33.6 percent of the total length in adult T. proximus and 28.3 to 35.3 percent in adult T. sauritus. Sexual dimorphism in proportionate tail length is evident in both species.

Osteology

Hypapophyses are present throughout the length of the vertebral column as is characteristic of natricine snakes. (Malnate, 1950, however, has described a new genus which is apparently closely related to the natricine genus Regina, but lacks hypapophyses on the post-thoracic vertebrae). The skull is similar to that of other species of the genus. Certain differences do exist, but these can best be analyzed by a comparative study of the skulls of all species of Thamnophis, and that is a problem beyond the scope of the present investigation. Members of the sauritus group have the greatest number of teeth on each tooth-bearing bone of any species in the genus for which data are available. The number of maxillary teeth ranges from 27 to 34, palatine teeth from 19 to 41, pterygoid teeth from 29 to 36, and dentary teeth from 33 to 36. Table 1 shows the frequency distribution of maxillary teeth

TABLE 1.—Individual variation in maxillary dentition in the *Sauritus* Group

Species	Males	Females
ornatus	27	27
	28(2)[a]	28(2)
	29(2)	29(3)
	30(6)	30(6)
	31(2)	31(2)
	32	32(2)
	34(2)	
sauritus	27	27(2)
	28	28(2)
	29(4)	29(3)
	30	30(2)
	31	

[a]Figures in parentheses on this and subsequent tables indicate the number of individuals when there is more than one.

counts (too few counts are available for the other bones for a frequency distribution table to have any significance). Some sexual dimorphism may be present, the males having a slightly greater number of maxillary teeth on the average. The maxillary teeth increase only slightly in length posteriorly, but the last three teeth are abruptly enlarged.

Hemipenis

The hemipenes of T. proximus and T. sauritus are virtually identical in all respects and are the smallest known for the genus. For many species information is not available. The inverted organ usually extends to the eighth subcaudal, frequently to the seventh or to the ninth, and in only one instance to the ninth (Table 2). Peters (1960) noted a negative correlation between relative tail length and hemipenis length in certain dipsadine snakes, and it appears that the same phenomenon occurs in Thamnophis.

TABLE 2.--Hemipenis length in the sauritus group

Sample	Hemipenis extends to subcaudal:	Sample	Hemipenis extends to subcaudal:
proximus	8(11)	sauritus	8 (2)
	7(14)		7 (1)
	9(10)		9(10)
	7 (1)		

Scutellation

The most distinctive feature in the scutellation of the Mauritus Group is the unusually large number of subcaudals in both species. These range from a minimum of 92 in *T. proximus* to a maximum of 136 in *T. mauritius*, almost always exceeding 100 in *T. mauritius* and less frequently exceeding that number in *T. proximus*. Only rarely do other species in the genus have more than 100 subcaudals, and usually the number is much less. Other important scale characters include: a single preocular; 2 supralabials entering the orbit; a maximum of 19 dorsal scale rows in 98.6 percent of the *T. proximus* and 99.3 percent of the *T. mauritius* examined; all dorsal scales strongly keeled, those of the outermost row not greatly enlarged.

Coloration

Both *T. proximus* and *T. mauritius* have vertical black bars on the labials and black markings on the venter, although in all *T. mauritius* and in certain populations of *T. proximus* there is an extension of brown pigment onto the lateral margins of the ventral scutes to form a dark ventrolateral stripe. A lateral stripe is always present on dorsal scale rows 3 and 4 (confined to row 3 posteriorly in one race of *proximus* and includes row 2 anteriorly in northern populations of *mauritius*), but the vertebral stripe is frequently lacking in some areas. The lateral stripe is usually a shade of yellow, white, or blue, the vertebral

stripe a shade of yellow, orange, red, or brown. The color between the stripes ranges from olive-grey and light brown to black. There is a broad, vertical yellow bar on each preocular.

Relationships

T. proximus and T. sauritus form a closely knit species group which does not show particularly close affinities to any of the other species complexes in the genus, although Ruthven (1908) suggests a relationship to the radix group--more specifically to Thamnophis eques. Such a possibility can be properly evaluated only within the framework of a comprehensive study of the interspecific relationships of the entire genus. For the present we can say that the relatively long tail, extreme reduction in spotting of the dorsum, and transitional syncranterian maxillary dentition[1] indicate that the members of the sauritus group are highly specialized, and that the group itself occupies an advanced evolutionary position within the genus Thamnophis. The large number of teeth present in sauritus and proximus is not here interpreted as being a primitive condition, but rather a secondary modification.

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[1] Transitional syncranterism is equivalent to the "continuous-abrupt" arrangement characterized by Malnate (1960) and thought to represent an evolutionary transition between the more generalized syncranterian and the more specialized diacranterian conditions.

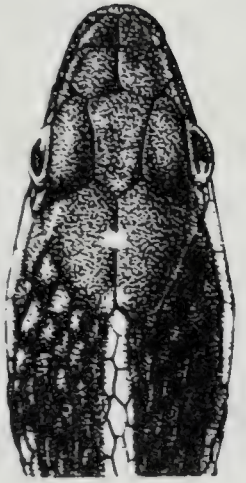
Species Accounts

Key to the Species

Parietal spots almost always present, fused, bright and usually fairly large (Figure 1A, left); brown pigment usually not extending onto ventral scutes to form a dark ventrolateral stripe on each side or, if present, covering less than 2/5 of the area of each scute (except in the Chiapas Highlands); mean muzzle length/frontal length for any given population usually greater than 0.70 . . . . . *proximus* (p. 18)

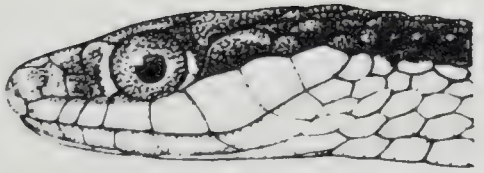
Parietal spots frequently lacking, when present they are small and rarely fused or bright (Figure 1A, right); brown pigment always extending onto ventral scutes and usually covering 2/5 or more of the area of each scute; mean muzzle length/frontal length usually less than 0.70 . . . . . *sauritus* (p. 92)

Figure 1.--Head patterns in the two species of the Maritus group in dorsal view (A) and lateral view (B).



A

A



B

B

PROXIMUS

SAURITUS

The Western Ribbonsnake

Thamnophis proximus (Say)

Coluber proximus Say, 1823: 339

Tropidonotus proximus Hole, 1827: 535

Eutainia Fairayi Baird & Girard, 1853: 25

Eutainia proxima Baird & Girard, 1853: 25

Eutaenia proxima Baird, 1859: 16

Eutaenia rutiloria Cope, 1885: 360

Thamnophis proximus Garman, 1892: 105

Thamnophis proximus Strecker, 1907: ---

Eutainia rutiloria Cochran, 1961: 162

Holotype

According to Smith and Taylor (1945) the holotype is lost. I do not know in which institution it had been deposited. It was collected in Nebraska at a stone quarry on the west side of the Missouri River, 3 miles above the mouth of Boyer's River (Iowa) by Long's expedition to the Rocky Mountains either in 1819 or 1820. In terms of presently existing towns, the type locality lies approximately 3 miles NNW Fort Calhoun, Washington County, Nebraska.

Definition

A large, long-tailed member of the genus Thamnophis

characterized by: 19-19-17 dorsal scale rows; a single preocular; typically 8 supralabials, the fourth and fifth entering the orbit; 141 to 161 ventrals; 82 to 131 subcaudals; lateral stripe on dorsal scale rows 3 and 4, at least anteriorly; labials and ventrals without black markings; dark ventrolateral stripe absent or narrow in most populations; parietal spots fused, brightly colored, and usually large; hemipenis short, usually extending to the seventh or eighth subcaudal when inverted; maxillary teeth numerous, usually 30 to a side.

Range

The species is distributed from southern Wisconsin, Indiana, and the Mississippi Valley west through the Great Plains to southeastern Colorado and eastern New Mexico, south through eastern Mexico to central Costa Rica (Figures 2 and 3). It is present on the Pacific coast of Mexico near Acapulco, Guerrero, and on the Isthmus of Tehuantepec in Oaxaca. A western ribbonsnake (KUMNH 6179) collected in the 1800's and labelled simply Minnesota needs to be authenticated by further collecting. Hubbard (1947) records several specimens of T. proximus from north-central South Dakota. Thomas Uzzell has examined these specimens (USNM 74377, 74378-382) at my request and reports that they are actually Thamnophis radix. There are apparently no valid records of proximus in the Great Plains north of Thurston County, Nebraska.

Figure 2.—Distribution of Thamnophis proximus in the United States. Solid dots represent specimens examined; open circles are literature records. Stippled areas represent the probable zones of intergradation between subspecies.

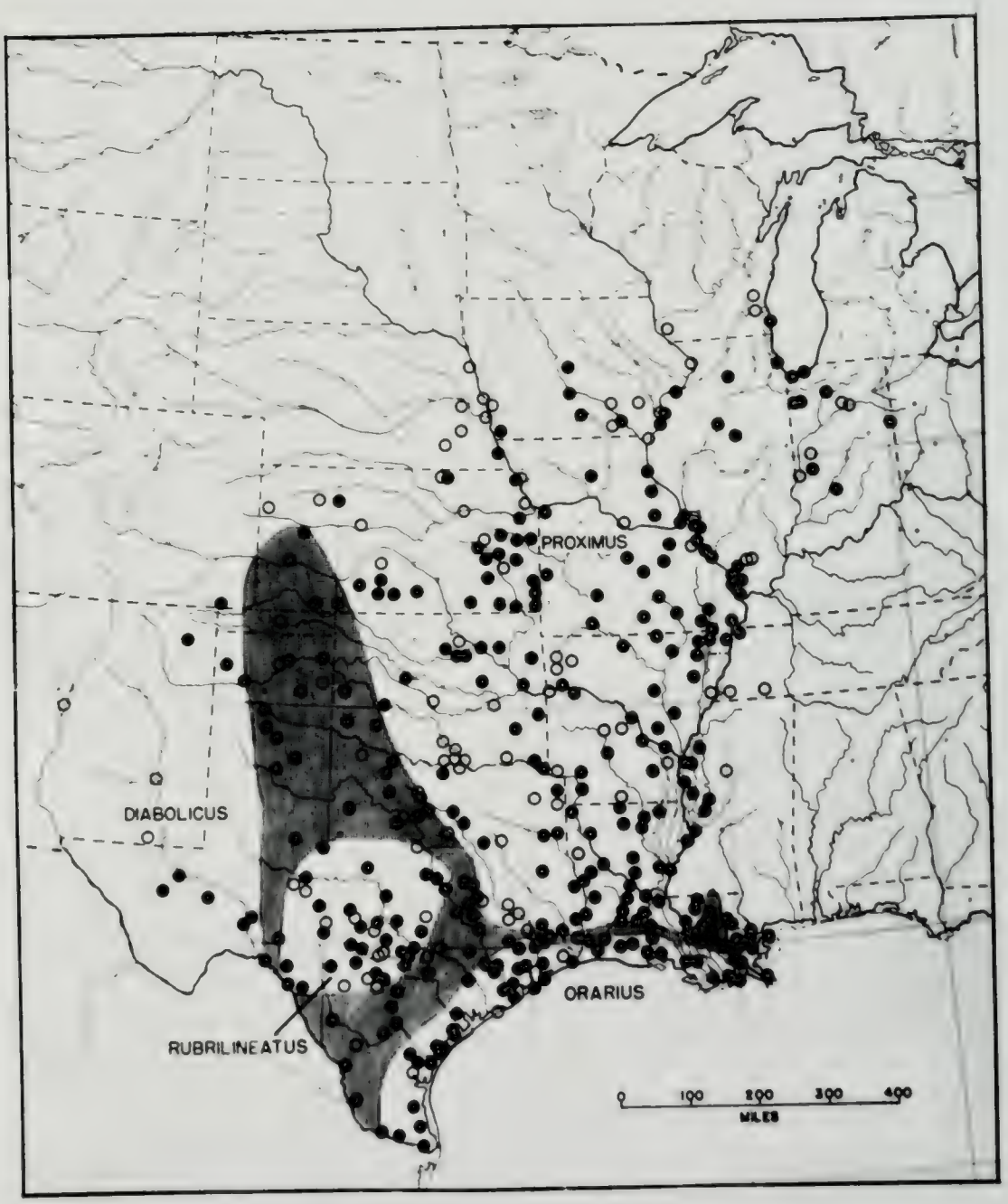
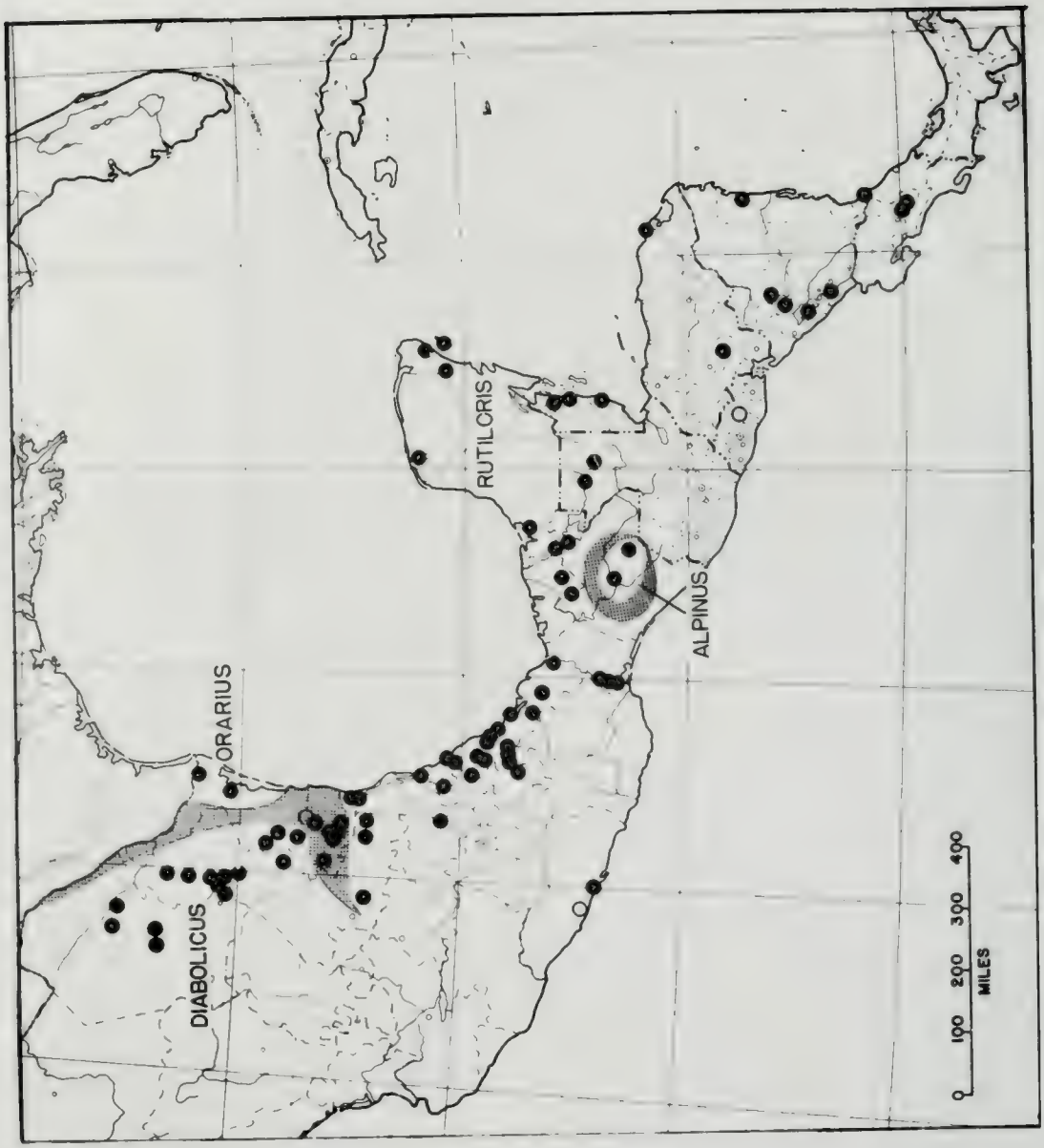

PROXIMUS
DIABOLICUS
ORARIUS
RUBRILINEATUS
0 100 200 300 400
MILES

Figure 1. Distribution of Dendroica virens in Mexico and Central America. Solid dots represent specimens examined; open circles are literature records. Dotted areas represent the probable zones of intergradation between subspecies.


DIABOLICUS
ORARIUS
RUTILCRIS
ALPINUS
0 100 200 300 400
MILES

Variation

Sexual Dimorphism

Distinct sexual differences exist in number of ventrals, number of subcaudals, and relative tail length. The amount of dimorphism in each of these characters varies from one local population to the next, and there appears to be no geographic correlation.

The difference in mean number of ventrals ranges from 0.3 of a scale in favor of the females in the sample from the Staked Plains of western Texas (the only sample with at least five individuals of each sex in which females have been observed to have more ventrals than the males), to more than 5 in favor of the males in certain other areas. Those populations from which at least 15 adults of each sex are available are compared in Table 3. There is a noticeable lack of geographic variation in the degree of dimorphism as expressed by the coefficient of divergence. Furthermore it may be noted by referring to Table 3 in Klauber (1943) that the degree of dimorphism exhibited in this character by members of the *mauritus* group is slight in comparison to most of the other forms for which comparable data are available. *Thamnophis proximus* shows greater sexual dimorphism in number of ventrals than does *Thamnophis [illegible]*, less dimorphism than *T. [illegible]* and *T. [illegible]*, and about the same amount as *Thamnophis brachystoma* and *T. mauritus* (Table 4).

Table 3.--Sexual dimorphism in ventrals in Thamnophis sauritus

Population	Males		Differences		Females	
	N	M	Dif	Coef	N	M
New Orleans area	35	173.6±0.50	3.2	1.86±0.05	52	170.4±0.39
East-central Texas	18	166.7±0.73	4.3	1.07±0.09	18	166.1±0.61
Edwards Plateau	34	167.3±0.46	3.9	2.33±0.10	30	163.9±0.74
Southern Texas	46	166.1±0.40	4.3	1.70±0.04	49	161.8±0.36
Chisos Highlands	15	161.7±0.59	3.7	2.31±0.08	22	158.0±0.55

N = number of individuals; M = mean; Dif = difference between means; Coef = coefficient of divergence expressed as a percent.

Table 4.--Coefficients of sexual divergence in six species of Thamnophis

Species	Origin of Sample	Ventrals (♀/♂)	Subcaudals (♀/♂)
T. [illegible][a]	Western Pennsylvania	2.00 ?	14.29 ?
T. elegans[b]	San Diego Co., Calif.	4.17±0.20	10.34±0.34
T. ordinoides[b]	Western Oregon	1.06±0.35	17.83±0.64
T. proximus	New Orleans area	1.86±0.05	9.03±0.20
	East-central Texas	1.87±0.03	---
	Edwards Plateau	4.31±0.10	9.16±0.13
	Southern Texas	1.76±0.04	6.83±0.26
	Chiapas Highlands	2.31±0.08	---
T. radix[b]	Cook Co., Illinois	4.01±0.36	14.44±0.71
T. sauritus	Southwestern Florida	3.31±0.13	6.03±0.29
	North-central Florida	4.31±0.19	8.45±0.39
	Southern Michigan	4.44±0.00	7.03±0.36

[a]Data from Burton (1956).

[b]Data from Klauber (1943).

Somewhat greater sexual differences exist in mean number of subcaudals. These mean differences range from 0.8 in favor of the females in the Galveston Bay, Texas, sample (the only one in which the males have fewer subcaudals than the females) to as much as 15.2 in favor of the males. Table 5 presents a comparison of those populations from which at least 15 adults of each sex are available. The amount of sexual dimorphism in subcaudal numbers is not great either in this species or in *T. sauritus* when their respective coefficients of sexual divergence are compared with those of many other colubrid snakes for which data are available (Klauber, 1943; Auffenberg, 1955; Duellman, 1958; Dowling, 1960; and others). The coefficients are even less, in fact than in other species of Thamnophis (Table 4) which is in keeping with the hypothesis that sexual dimorphism in subcaudals tends to be greater in short-tailed than in long-tailed species (Klauber, 1943).

Females average longer than males but usually have a proportionally shorter tail. The largest female examined (UMMZ 761 from Cameron County, Texas) has a body length of 900 mm. plus a 332 mm. incomplete tail. The largest male (UF 12161-4 from St. Charles Parish, Louisiana) has a body length of 553 mm. and an incomplete tail. Wright and Wright (1957) report animals with greater total lengths (1365 mm. female, 1119 mm. male), but do not give locality data. Adults of both sexes average well below these maxima.

TABLE 5.—Sexual dimorphism in mandibula in Lampropeltis getulus

Population	Males		Differences		Females	
	N	M	DM	D%	N	M
San Antonio area	10	117.6±1.24	10.2	9.05±1.14	33	107.6±0.91
Edwards Plateau	22	100.0±0.82	5.3	5.14±0.14	22	102.1±0.87
Southern Texas	14	108.1±1.17	7.0	6.66±0.48	13	101.1±0.82

N = number of individuals; M = mean; DM = difference between means; D% = coefficient of divergence expressed as a percent.

The mean difference in adult tail length/total length ratio ranges from 0.004 in favor of the females (Galveston Bay, Texas, being the only area where the ratio for females has been observed to be higher than that for males) to 0.022 in favor of the males. Mean tail length/total length values for males range from 0.275 to 0.318, for females from 0.270 to 0.313. As expressed by the muzzle length/frontal length ratio, females apparently have slightly longer muzzles than do males (see p. 51).

Caudodorsal scale row reduction reflects sexual dimorphism, males having the more posterior reduction. This is almost surely a consequence of the presence of the hemipenes and their retractor muscles in the proximal part of the tail. The reduction formulae for CAS 3091, an adult male from Comanche County, Oklahoma, and CAS 5099, an adult female from St. Charles County, Missouri, are presented below as examples. The formulas are slightly modified from the system proposed by Dowling (1951) in that the figures above the line represent the left side of the animal, those below the line the right.

CAS 3091 ♂

$$17\frac{-3(5)}{-2(1)} \quad 16\frac{-2(3)}{-2(2)} \quad 15\frac{-3(4)}{-3(4)} \quad 14\frac{-3(7)}{-3(7)}$$

$$13\frac{-4(12)}{-4(12)} \quad 12\frac{-3(20)}{-3(24)} \quad 11\frac{-3(30)}{-3(34)} \quad 10\frac{-4(100)}{-4(104)} \quad 9(113)$$

CAS 5099 ♀

$$17\frac{-4(4)}{-3(1)} \quad 16\frac{-4(4)}{-3(2)} \quad 15\frac{-4(7)}{-4(4)} \quad 14\frac{-4(7)}{-4(6)} \quad 13\frac{-4(10)}{-4(10)}$$

$$12\frac{-3(13)}{-3(13)} \quad 11\frac{-4(86)}{-4(89)} \quad 10\frac{-4(96)}{-4(98)} \quad 9(99)$$

Ontogenetic Variation

Newly born *T. proximus* have a proportionally shorter tail than the adults (Table 6), but differential growth must be rapid during the first year inasmuch as subadults have essentially the same tail length/total length values as adults of the same population.

Individual Variation

Characters which neither vary geographically nor show sexual or ontogenetic variation are discussed below. Data on head scales refer to one side only. Individual variation in meristic characters is summarized in Table 7.

Scales

There is 1 preocular and usually 3 postoculars. The most frequent variation is the appearance of a fourth postocular on one or both sides. Of 1446 *T. proximus*, only one individual has an extra preocular and that on one side only. It is interesting to note the stability of this character in the *Saurites* Group in view of its extreme variability in a number of the other species of *Thamnophis* (Ruthven, 1908; Fitch, 1940).

Temporals

One large anterior temporal and 2 slightly smaller posterior temporals is the usual condition, but there is greater individual variation in this character than in any other, most frequently an increase in number. Although the

TABLE 6.—Ontogenetic change in tail length/total length ratio in the Notropis procne group

Species and localities	Males		Females		Coef.	
	Juv.	Adult	Juv.	Adult	male	female
N. amabilis						
New Orleans area	.299	.317	.308	.302	5.34	4.75
N. mauritius						
Southern Florida	.334	.347	.338	.340	3.82	0.59
Intermediate peninsular Florida	.322	.343	.340	.340	6.32	0.00
Northern Bay drainage	.329	.343	.345	.341	7.04	4.93

Coef. = coefficient of ontogenetic divergence expressed as a percent

TABLE 7.—Individual variation of meristic characters in *Haplochromis strigigena*

Fin-rays	Dorsal spines	Anterior branched rays	Posterior branched rays	Anterior lateral-line scales	Posterior lateral-line scales	Transverse scale rows	
Males							
I(653)[a]	X (2)	I (386)	I (14)	6	8,9	I (2)	17-18-17
	X,3 (8)	I,2 (34)	I,2 (19)	7 (18)	9 (14)	2(5)	17-19-15
	3 (605)	2 (30)	2 (548)	7,8 (35)	9,10 (20)	3 (71)	17-1 -17(2)
	3,4(34)		2,3 (22)	8 (600)	10 (57)	4 (2)	18-1 -17(2)
	4 (5)		3 (24)	8,9 (8)	10,11(10)	5	18-17-16
					11 (14)		19-17-17(4)
							19-18-17
							19-19-15(2)
							19-19-16
Females							
I(754)	X (2)	I (671)	I (11)	6	8 (2)	I (29)	17-19-17(2)
I,2	X,3 (5)	I,2 (64)	I,2 (13)	7 (15)	9 (11)	2(30)	18-19-16
	3 (704)	2 (56)	2 (573)	7,8 (82)	9,10 (35)	3(140)	18-19-17
	3,4(62)		2,3 (187)	8 (766)	10 (20)	4 (12)	19-17-17(5)
	4 (24)		3 (43)	8,9 (13)	10,11(30)	5	19-18-17
	4,5			9 (5)	11 (13)	6 (2)	19-19-15
					11,12	6	19-19-16

[a] Single numbers indicate that both sides of the head have the same count; the number within the parentheses is the number of individuals when there is more than one.

the occurrence of 2 anterior temporals is common, only one of them, the lower, is ever in contact with the postoculars. In addition to an increase in the number of scales, the anterior portion of the anterior temporal is occasionally fragmented to form 1 or 2 small scales which are rarely much larger than the postocular scales. There appears to be a higher incidence of this variation in the Chiapas highlands than in any other area (42 percent of the animals examined have this fragmentation of the anterior temporal on one or both sides of the head).

Supralabials

Eight is the usual number, the fourth and fifth entering the orbit. Seven apparently occurs by loss of a preorbital supralabial, 9 by addition of 1 posterior to the orbit. Infrequently there are small scales wedged between 2 of the normal scales either at their upper or lower margins. Rarely an individual supralabial will be partially divided by an incomplete suture.

Infralabials

Ten is the usual number, 9 and 11 being equally common as variations. Nine usually occurs as the result of the elimination of the suture between the third and fourth or the eighth and ninth infralabials, in that order of frequency. Eleven usually results from a division of the third infralabial. As in the supralabials, small anomalous scales are occasionally interposed between normal ones.

Intergenials

There are usually 4 small scales arranged in a linear sequence between the genials. There may be as few as 1 or as many as 6. When several are present, some may be paired rather than all being in a linear series of singles. Fifty percent of the individuals in the Chiapas highlands sample have more than 4 intergenials, an unusually high incidence. These animals also have a high frequency of anterior temporal fragmentation; over 76 percent of the series examined have one or both of these anomalies.

Ventrals

Anomalous divisions or partial duplications of ventral scutes, largely caused by partial duplication of vertebrae, occur in many groups of snakes (Klauber, 1939), and the Mentalis Group is no exception. All of the types illustrated by Peters (1960) in his study of the subfamily Bipsadinae occur in both proximus and mentalis, the most common type being one in which 1 or more anomalous partial scutes are inserted between the terminal ventral and the anal plate. This type occurs in 9.5 percent of the proximus examined in this study. An additional 4.3 percent (including a few of those just mentioned) have partial scutes at some other point on the venter. Barton (1953) reports that 19.5 percent of the specimens of L. bracestoma which he examined have either ventral or subcaudal anomalies.

Subcaudals

Of the individuals examined, 2.3 percent have 1 or more sets of fused subcaudals (i.e., there is no longitudinal suture separating the 2 adjacent members of a subcaudal pair). Barton's (1956) comments on this condition in *L. brachystoma* are noted above.

Dorsal scale rows

Only 4 percent of the snakes examined differ from the typical formula of 19-19-17. A large majority of the individuals having more than 19 rows at any point on the body are from the delta region of the Mississippi River. They make up only a small part of that population, however, in contrast to the population in the vicinity of Orizaba, Veracruz, in which 31 percent of the specimens examined have reductions in the dorsal scale row formula (i.e., 17-18-17, 18-19-16).

Dorsal scale row reduction

Reduction in the number of dorsal scale rows is, in all but four of the 18 specimens checked for this character, the result of loss of row 4 on both sides of the body. Of the four exceptions, one lost row 4 on one side, 4 or 5 (impossible to say which) on the other; one lost row 4 or 5 on both sides; one lost row 4 on one side, 5 on the other; and one lost row 5 on both sides.

Among males the reduction takes place opposite ventrals 83 through 105, mean 93.8, among females from ventral 78

through 167, mean 90.6. There appears to be a positive correlation between the total number of ventrals and the point of reduction, the greater the number the more posterior the reduction. Consequently, the point of reduction will of necessity vary geographically to a certain degree. It also imposes a certain amount of sexual dimorphism on the character since males almost invariably have more ventrals than do females.

Pattern and coloration

Size of the parietal spots varies individually, and some individuals have streaks of light pigment extending anteriorly from the parietal spots along the frontal-parietal suture and occasionally onto the frontal itself. Size, or even presence, of the postocular light spot and the black postorbital vitta varies individually as well as geographically. Presence or absence of a row of spots above the lateral stripe or of a black margin along the vertebral stripe also varies from individual to individual. Relative darkness of the dorsal ground color frequently varies in a similar manner.

Geographic Variation

In an animal the range of which extends from southern Wisconsin to central Costa Rica, a distance of about 3000 miles, it is not surprising to find a considerable amount of geographic variation. Because there is a lack of concordance among most of the geographically varying

characters, each will be considered separately. In the following discussion the term "population" is used in a biological sense and is not synonymous with the statistical term. "Deme" or "local population" would be more nearly equivalent to "population" as I am using it. A group of morphologically similar populations constitute a major population, which is in turn equivalent to the geographic subspecies. Meristic and proportional values discussed below are based on population samples, and this fact is to be inferred when not actually stated in the text. Such samples when of an adequate size may reasonably be expected to represent the population from which they were collected.

Ventrals

The mean ventral counts are remarkably constant east of the Mississippi River, from western Indiana to north of Lake Pontchartrain in Louisiana (see Figure 4). The means for males fall between 170.4 and 171.8, for females between 168.9 and 169.0. South and west of Lake Pontchartrain in and adjacent to the Mississippi delta region the number of ventrals increases slightly, the means ranging from 171.9 to 174.1 in males, and from 168.9 to 171.4 in females. The highest means in both sexes occur near the mouth of the Mississippi River.

West and southwest, from the Mississippi Valley to the Rio Grande Valley, the mean number of ventrals decreases gradually and in a relatively uniform fashion, there being

Figure 4.--Geographic variation in ventral number of Hyperoglyphe perciformis in the United States. Black blotches represent the areas from which samples were taken. The upper numbers associated with each blotch are the sample mean and sample size (in parentheses) for males; the lower numbers present the same data for females. When a line appears in place of either the upper or lower numbers, it signifies that no specimens of that sex were present in the sample.

167.5(4)
166.3(10)
173.0(4)
168.5(6)
169.0(3)
166.5(4)
169.9(11)
166.8(5)
171.0(6)
168.1(7)
165.3(3)
165.7(3)
167.6(13)
164.4(17)
171.6(9)
167.4(9)
168.6(8)
166.9(9)
170.0(4)
165.6(10)
170.8(11)
168.7(12)
168.7(6)
164.5(6)
166.4(9)
165.9(10)
165.6(5)
164.2(12)
167.8(6)
167.0(10)
170.8(6)
168.5(8)
172.5(4)
165.8(12)
168.3(6)
167.4(8)
170.8(6)
167.6(13)
166.7(7)
167.0(5)
163.5(2)
163.0(4)
168.9(12)
168.1(11)
170.5(11)
169.0(10)
167.6(5)
162.5(11)
170.1(10)
166.1(8)
170.5(6)
167.0(9)
168.6(3)
167.3(10)
168.8(17)
167.3(12)
167.3(7)
165.0(10)
170.8(4)
165.9(8)
168.9(18)
166.1(18)
170.4(18)
168.1(14)
167.8(10)
164.5(10)
A
B
171.8(8)
166.9(10)
167.3(7)
163.5(8)
166.9(9)
164.6(35)
173.6(35)
170.4(52)
166.9(10)
164.5(24)
169.7(10)
165.8(12)
171.9(37)
168.9(40)
174.1(15)
171.4(10)
166.3(6)
166.2(5)
167.9(8)
165.6(8)
167.6(34)
163.9(30)
168.4(7)
164.0(7)
A 169.4(9)
167.7(3)
B 151 (1)
158.2(9)
167.3(9)
163.9(16)
0 100 200 300 400
MILES
166.6(46)
163.7(49)

a certain amount of variation from one population to the next. A population in western Louisiana (Figure 4,2), however, shows more than the expected divergence in that the sample mean in females (only one male is available) is from 7 to 9 scales less than in females from populations less than 45 miles distant. It is perhaps significant that all the localities from which specimens of this population are available are associated with relict prairie areas.

Southward from the Rio Grande Valley the mean ventral counts decrease only slightly in the Sierra Madre Oriental, but fall off sharply in the coastal plain of Tamaulipas (see Figure 5). There is a difference of almost 10 ventrals in the means of females (about 3 ventrals in males) from the lower Rio Grande Valley and those from southern Tamaulipas, a distance of little more than 400 miles. There is essentially no change in the mean for females and only a slight decrease in that for males over the 400-mile stretch from southern Tamaulipas to central Veracruz, but within the succeeding 50 to 75 miles southward along the coast to the vicinity of Ciudad Veracruz, the means for both sexes decrease by almost 4 scales.

The number of ventrals is lowest in the Tabasco-Campeche lowlands where the mean for males is 142.3, for females 144.9. This represents a decrease of almost 6½ scales in males and 4½ in females over the 300-mile distance from south-central Veracruz. A small series from Isla Aguada Campeche has counts which indicate that ventral numbers in

Figure 3.--Geographic variation in several measures of Ammodramus grammacus in Mexico and Central America. Black blotches represent the areas from which samples were taken. The upper numbers associated with each blotch are the sample mean and sample size (in parentheses) for males; the lower numbers present the same data for females. When a line appears in place of either the upper or lower numbers, it signifies that no specimens of that sex were present in the sample.

163.5(12)
158.4(12)
164.0(12)
161.4(11)
157.8(6)
155.8(5)
162.3(4)
157.8(4)
159.0(10)
153.8(8)
158 (1)
152.0(4)
156.6(9)
153.2(13)
153.0(13)
149.3(11)
159.1(8)
157.0(6)
155.0(2)
146.6(5)
144.9(8)
158.1(13)
154.4(16)
153 (1)
148 (1)
152.0(4)
161.7(15)
158.0(22)
146.0(5)
149.7(10)
147.4(12)
153.6(9)
150.2(6)
0 100 200 300 400
MILES

this region probably averages somewhat higher than in adjacent areas. From the Tabasco-Campeche area to the northern tip of the Yucatan Peninsula there is a slight increase, and along the 1000 miles of Caribbean coastland from Cozumel Island to Boca del Rio, Costa Rica, the mean number of ventrals remains essentially constant.

The picture is not yet complete, however, because the western ribbonsnake is not limited to the coastal plain in tropical America, but is also found in the Sierra Madre Oriental at altitudes up to 6500 feet, in the Chiapas highlands up to 7500 feet, and on the Pacific side of the Central American uplands up to 5000 feet. The majority of high-altitude populations of Thamnophis proximus have a mean number of ventrals markedly different from that of their geographically adjacent lowland counterparts. However, rather than having a decreased number as one might predict on the basis of the temperature-scutellation studies of Fox (1948) and Fox, Gordon, and Fox (MS) on T. sirtalis, the number of ventrals increases. Furthermore, the amount of increase seems roughly correlated with the amount of increase in altitude. This seems particularly true of three populations in south-central Veracruz, the extremes of which are only 65 airline miles apart, which range in altitude from sea level to 5500 feet. In the vicinity of Ciudad Veracruz, males have 153.0 mean ventrals, females have 149.3. Near Cordoba (2000-3000 feet) the means are 5 scales greater in

both sexes. In the sample from the Orizaba area (4000-5900 feet) the mean for males is only 1 scale more than at Cordoba; in females it is about 2½ scales.

The population in the Chiapas Highlands has a greater mean number of ventrals (almost 8 higher in both sexes in the series examined) than the Central American upland population. However, inasmuch as the two are widely separated geographically, factors other than altitude may be involved. On the other hand, the means for samples from the Central American upland population are 3 to 4 scales greater than means for the Caribbean lowland animals, and means for the Chiapas Highlands series are 13 to 15 scales more than for the Tabasco-Campeche lowlands population, 100 miles to the north and some 7000 feet lower in elevation. This relationship between high ventral count and high altitude does not hold true north of the Orizaba-Cordoba area. A small series from the vicinity of Jalapa, Veracruz (3900-4500 feet), a juvenile female (CNHM 103445) from 6 miles S Nacuiltipan, Hidalgo, and a subadult male (CNHM 18919) from near Tenuitlan, Puebla (approximately 6500 feet), agree well with specimens from the coast at the same latitude.

There are other populations, unfortunately represented by only a handful of specimens, which do not fit at all well into the variational pattern described above. Four females from eastern San Luis Potosí agree in their mean number of ventrals with the south-central Veracruz females

rather than with those in the intervening area. Two females (UMMZ 41555-556) from Cuatotolapam in southern Veracruz have a mean almost 6 scales higher than that of the population less than 50 miles to the northwest, and 10 scales greater than in the Tabasco-Campeche population barely 200 miles to the east. There may be some significance in the fact that this locality is not far from Los Tuxtlas, an isolated mountain range in the middle of the coastal plain, noted for having faunal associations strikingly different from those of the coastal plain which surrounds it.

Subcaudals

Although the general pattern of reduction in subcaudal number is similar to that of the ventrals, many of the details are strikingly dissimilar. Whereas in ventrals the populations throughout the Mississippi Valley have essentially the same mean, and reduction in number occurs southwestward, in subcaudals the highest means are centered in southeastern Louisiana (both to the north and south of Lake Pontchartrain) and the number of subcaudals decreases fairly uniformly and rapidly northward east of the Mississippi River, northwestward into the Great Plains, westward through central Texas, and along the Gulf Coast into Mexico (see figures 6 and 7). The mean number of subcaudals in western Indiana is about 12 to 14 scales less than in southeastern Louisiana; means in central Kansas are 10 to 12 less; and the series representing the Edwards

Figure 6.--Geographic variation in subcaudal number of Thamnophis ordinoides in the United States. Black blotches represent the areas from which samples were taken. The upper numbers associated with each blotch are the sample mean and sample size (in parentheses) for males; the lower numbers present the same data for females. When a line appears in place of either the upper or lower numbers, it signifies that no specimens of that sex were present in the sample.

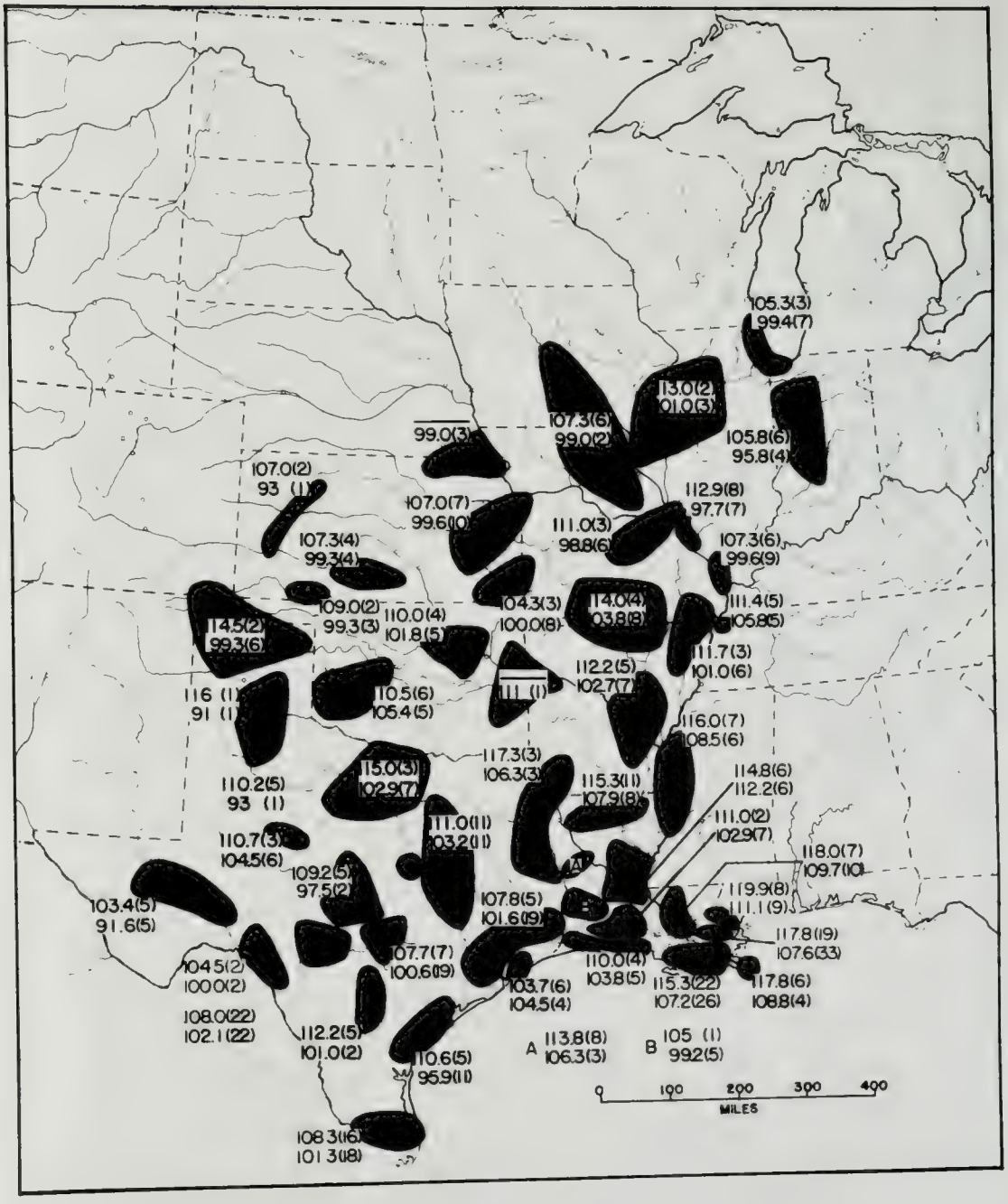

105.3(3)
99.4(7)
113.0(2)
101.0(3)
107.3(6)
99.0(2)
99.0(3)
105.8(6)
95.8(4)
107.0(2)
93 (1)
112.9(8)
97.7(7)
107.0(7)
99.6(10)
111.0(3)
98.8(6)
107.3(6)
99.6(9)
107.3(4)
99.3(4)
109.0(2)
99.3(3)
110.0(4)
101.8(5)
104.3(3)
100.0(8)
114.0(4)
103.8(8)
111.4(5)
105.8(5)
114.5(2)
99.3(6)
111.7(3)
101.0(6)
112.2(5)
102.7(7)
116 (1)
91 (1)
110.5(6)
105.4(5)
111 (1)
116.0(7)
108.5(6)
117.3(3)
106.3(3)
115.0(3)
102.9(7)
110.2(5)
93 (1)
115.3(11)
107.9(8)
114.8(6)
112.2(6)
111.0(2)
102.9(7)
111.0(11)
103.2(11)
110.7(3)
104.5(6)
118.0(7)
109.7(10)
109.2(5)
97.5(2)
119.9(8)
111.1(9)
103.4(5)
91.6(5)
107.8(5)
101.6(9)
117.8(19)
107.6(33)
107.7(7)
100.6(9)
110.0(4)
103.8(5)
104.5(2)
100.0(2)
115.3(22)
107.2(26)
117.8(6)
108.8(4)
103.7(6)
104.5(4)
108.0(22)
102.1(22)
112.2(5)
101.0(2)
A 113.8(8)
106.3(3)
B 105 (1)
99.2(5)
110.6(5)
95.9(11)
0 100 200 300 400
MILES
108.3(16)
101.3(18)

Figure 7.--Geographic variation in subcaudal number of Tantilla proxima in Mexico and Central America. Black blotches represent the areas from which samples were taken. The upper numbers associated with each blotch are the sample mean and sample size (in parentheses) for males; the lower numbers present the same data for females. When a line appears in place of either the upper or lower numbers, it signifies that no specimens of that sex were present in the sample.

100.8(5)
93.0(5)
105.7(6)
96.0(6)
110.0(2)
98 (1)
102.5(4)
97.5(2)
101.3(6)
91.0(6)
92.0(3)
101 (1)
93.0(7)
97.6(7)
89.7(9)
98.0(4)
92.0(4)
99.0 (4)
93.7(11)
93.0(2)
91 (1)
87.4(5)
100 (1)
92.3(3)
84.0(2)
100.9(9)
92.9(17)
96.0(6)
91.0(5)
97.8(5)
92.0(2)
0 100 200 300 400
MILES

Plateau population has 8 to 9 fewer mean subcaudals in females (10 to 12 in males), as does the sample from southern Texas.

West of the Pecos River the number of subcaudals decreases sharply, the mean for females being 10 scales less than on the Edwards Plateau less than 200 miles to the east. The Coahuilan desert population is similar to the trans-Pecos animals in subcaudal number, more so in fact than to the geographically nearer Nuevo Leon population. Along the Gulf Coast of Texas, two populations show a rather anomalous variance from the pattern described above. The sample mean for Galveston Bay area females fits rather well into the sequence of reduction along the coast which was previously mentioned, but the mean for males is almost 7 scales less than for the populations on either side of the Galveston Bay area (it is even less than the mean for females from the same population). Scarcely more than 150 miles farther down the coast the situation is completely reversed. The males have the expected complement of subcaudals while the mean for females is from 5½ to 8½ scales less than in adjacent populations.

In south-central Tamaulipas, at about the latitude of the Tropic of Cancer, there is a sharp drop in the number of subcaudals, the means decreasing by 8 or 9 scales within a distance of less than 100 miles. From thence southward and eastward to the Tabasco-Campeche area the decline in subcaudal number again appears to be fairly uniform and

gradual (there may be a fairly steep drop in the mean for males between south-central Veracruz and Tabasco-Campeche, but only one specimen with a complete tail is available from the latter population). The lowest mean number of subcaudals in T. pranimus apparently occurs in northern Yucatan. There is a marked increase in subcaudals in the Caribbean lowlands, but more comparative material is needed from the Gulf side of the Yucatan Peninsula to determine the degree of increase.

Subcaudal number apparently is less well correlated with altitude than is the number of ventrals. There is virtually no difference in the means of males from sea level and of those from an altitude of 5000 feet in south-central Veracruz, and only a 2-to 4-scale increase in females from high altitudes. Females from the Caribbean lowlands, Central American uplands, and the Chiapas Highlands show no major differences although the high-altitude populations do have slightly higher means. The males from these populations may demonstrate altitudinal variation more clearly, although once again it should be remembered that the Chiapas snakes are separated from the other two groups geographically as well as altitudinally. The fact that the Isthmian Oaxaca series (all from less than 700 feet altitude) has means almost identical to those of the high-altitude Chiapas snakes underscores the need for caution in interpretation.

Proportions

Relative tail length (as expressed by the tail length/total length ratio) is, with a few notable exceptions, remarkably uniform over most of the range of L. getulus, making allowances for the usual interpopulation variation. Because many populations are represented by only a few specimens of either sex having tail length/total length values available, the following discussion can give at best only an approximation of the actual situation.

The snakes with the proportionally longest tails are found in the lower Mississippi Valley, the means for males ranging from 0.312 to 0.316 and for females from 0.301 to 0.313 (except those from southwest of New Orleans and in the Atchafalaya delta region which have 0.296). There is, in this area at least, a strong correlation between relative tail length and the number of subcaudals. This correlation is weak or nonexistent in many parts of the range. East of the Mississippi River the means vary within these extremes north to the Ohio River. West of the Mississippi River, populations having comparable means extend from the lower Mississippi Valley northward and westward through Arkansas and southern Missouri to the limits of the Ozark Plateau (the means for females, however, do decrease in the Ozark region).

Beyond this circumscribed area, the snakes have somewhat shorter tails, the means for males (with but one exception) falling between 0.290 and 0.308 (usually between

0.296 and 0.303). The one notable exception is the Chiapas Highlands population in which the nine males examined have a mean of 0.275. The lowest mean tail length/total length value for females, 0.270, also occurs in this population. Females from outside of the "long-tailed" area have means which range from 0.279 to 0.296 (usually from 0.289 to 0.297); but in addition to the Chiapas females already mentioned, those from trans-Pecos Texas (also 0.270) have shorter tails than are present in adjacent populations.

Relative muzzle length as expressed by the muzzle length/frontal length ratio is apparently subject only to interpopulation variation throughout most of the range of T. proximus. The Chiapas Highlands population, however, in this as in so many other features, is different from all other populations, particularly those adjacent to it. Chiapan males have a mean of 0.681, females 0.694. Means for four or more males from other populations range from 0.701 to 0.849 (mean 0.744), for females from 0.711 to 0.838 (mean 0.759).

Pattern

The fused parietal spots attain their largest relative size in northern Mexico and adjacent Texas; in some individuals they occupy half the length of the interparietal suture, as in AMNH 67336 from Nuevo Leon. In this area there is also a high incidence of light areas or streaks extending forward from the parietal spots and forking out

for varying distances along the frontal-parietal suture. In the Chiapas Highlands the parietal spots are incompletely fused and their anterior edges diverge at about a 30-degree angle from the interparietal suture, giving the entire arrangement the appearance of a thick chevron. This condition occurs sporadically throughout the range in individual snakes but it is present in 70 percent of the Chiapas specimens.

In most populations the postocular light spot occupies all of the lower, and varying amounts of the middle, postocular. In the southern part of the range from trans-Pecos Texas to Coahuila and Nuevo Leon, and in the coastal plain from the Tropic of Cancer to Central America, the postocular light spot is frequently absent and when present it is usually not brightly colored. The spot is also lacking in an occasional individual from more northern populations.

The broad black postorbital vitta typical of F. semiritus is usually lacking in tropical American specimens of F. proximus. When present, the stripe is frequently narrow and does not extend onto the postocular scales. Throughout the rest of the range, the presence or absence of the vitta, and its extent, varies individually.

In the lowlands of Mexico and Central America and along the coast to the lower Mississippi Valley, the vertebral stripe is usually broad and incorporates, in addition to the vertebral row of scales, more than half the

width of each paravertebral row. Frequently it covers all of both paravertebral rows. UMMZ 94469 from near Ciudad Mante, Tamaulipas, has the vertebral stripe covering the entire vertebral-paravertebral series and a small portion of row 5 as well. Outside of this area the stripe rarely includes more than half the width of each paravertebral row and it is often somewhat narrower, particularly in the extreme northern part of the range.

Mexican and Central American specimens are also characterized by having a narrow lateral stripe, the stripe occupying less than half of one of the 2 scale rows on which it is situated and varying amounts of the other row, usually slightly more than half. Furthermore, the stripe becomes even narrower beyond the point of dorsal scale row reduction, the stripe then being largely confined to the third row, but usually covering a small portion of row 4. The Chiapas Highlands population characteristically has the stripe involving only the third row posteriorly. Only about one-half of the snakes in the Nuevo Leon series have this reduction of the lateral stripe. North of the Rio Grande the lateral stripe almost invariably occupies more than half of both rows 3 and 4 and it does not become noticeably reduced posterior to the loss of row 4.

The dark ventrolateral stripe, which is found in all specimens of I. sauritus, and is the most reliable single character for distinguishing between the two species in the areas of sympatry (Rossman, MS), is well developed in certain

populations of L. proximus. It is present in the Chiapan highlands where the width of each stripe is 1/7 to 1/4 (usually 1/6 to 1/5) the width of a ventral scale. The stripe is slightly narrower in the Central American uplands, still narrower in the lowlands of Central America and Mexico, and usually disappears altogether north and west of central Texas.

Coloration

Cope (1885) described a ribbonsnake from Cozumel Island, Quintana Roo, Mexico, as having reddish orange labials. While I have not seen a western ribbonsnake with that particular labial color, living specimens from British Honduras, Chiapas, Veracruz, and eastern San Luis Potosí do have yellow-orange labials as opposed to the greenish white or greenish yellow ones present in individuals from Coahuila, Nuevo Leon, and the United States.

Due to a dearth of color descriptions in the literature, or accompanying museum specimens, and to limited availability of series of live snakes from throughout the range of the species, the following discussion can only delimit the geographic distribution of the different variations in the color of the dorsum, vertebral stripe, and lateral stripe in a general and approximate fashion. A more precise definition of the geographical extent of each color variation will need to be worked out on a local basis.

Specimens from Coahuila, Nuevo Leon, and apparently trans-Pecos Texas (the latter were not seen in life) have

an olive-grey dorsum. Throughout the rest of Mexico and Central America, the dorsum is more of an olive-brown; Chiapas Highlands examples are an exception having a color ranging from dark to very dark brown. The olive-brown of Central American snakes, as well as several other shades of brown, occur in southern and central Texas and along the Gulf coast of Louisiana and Texas. It apparently is found northward through the Texas panhandle to southeastern Colorado. Where brown-dorsum snakes come in contact with black ones, populations appear to be intermediate in their dorsal color. The black form is found from central Kansas, central Oklahoma, and eastern Texas northward and eastward throughout the rest of the range.

The orange vertebral stripe has the most extensive geographic distribution, being replaced by another color only in tropical America, on the Edwards Plateau, and in coastal Texas and Louisiana. Ribbonsnakes on and in the vicinity of the Edwards Plateau have a bright red vertebral stripe. Where brown-dorsum populations occur along the Gulf coast of Louisiana and Texas, the stripe is usually a gold or greenish gold in color. It infrequently has an orange cast. The stripe color is also gold in the Chiapas Highlands. A recently collected specimen (UF 12213) from near Acapulco, Guerrero, has a stripe which appears to be pale yellow; the color may have been gold in life. Snakes from Central America and that portion of Mexico not already discussed, i.e. the southern and central Gulf Coast and

adjoining uplands, have a greyish tan vertebral stripe which may appear to have a metallic luster.

Throughout most of the range of T. proximus, the lateral stripe is usually some shade of light yellow, although it is generally pale in lowland Mexico and Central America. Two specimens from Brazos County, Texas (UF 12193), are unique in having a lateral stripe that in life was bluish green on the neck and greenish white posteriorly. It is not known whether the condition is characteristic of the entire population or occurs merely as an individual variation. One of these two specimens also had a gold-colored vertebral stripe; the other had the orange stripe typical of this area.

Discussion

It is obvious that much of the geographic variation observed in T. proximus is of the discordant type; almost all the characters which I have discussed vary independently of each other, some being constant throughout a geographical area in which one or several of the other characters undergo radical change. This discordant variation is what would be expected, however, unless all of these characters are genetically linked, thus requiring certain combinations to be selected as a single unit. This does not seem likely, and it is more probable that each character is subject to independent selection by the environment (Tilden, 1961). There are two areas in which marked changes do take place

in a number of characters essentially simultaneously--the Chiapas Highlands and southern Tamaulipas at about the latitude of the Tropic of Cancer.

In the Chiapas Highlands almost every character which varies geographically except subcaudal number and labial color) takes on an aspect different from that in the adjoining areas. The high-altitude Chiapas population apparently has been at least semi-isolated from the lowland populations for a long period of time. The amount of gene flow between them at present must be minute. This isolation, whether partial or complete, coupled with adaptations for the rigorous existence imposed by living at high altitudes and perhaps furthered by genetic drift, has led to these snakes becoming different in many respects from the stock from which they have been derived.

The abrupt transition of characters in southern Tamaulipas coincides with the transition between the Neotropical and Nearctic faunal regions, an area noted for sharp faunal breaks. Ventral number, subcaudal number, labial color, vertebral stripe color, and lateral stripe color and width all change markedly at this point.

Southern Louisiana might be considered a third and rather minor area of concordance. Color of the dorsum, vertebral stripe width, and vertebral stripe color change over a relatively narrow zone between the coast and the interior.

In studying geographic variation in the various characters, one is struck by the fact that the number of ventrals and subcaudals is usually much more apt to undergo local fluctuations than are the elements of color pattern. The reason for the greater observable variability of these meristic characters is not known. Possibly they are not subject to as rigorous selective pressure as is color pattern, and consequently are less stable.

Taxonomy

The population samples discussed above group themselves into six fairly well-defined major populations which occupy discrete geographic areas and appear to deserve taxonomic recognition.[1] While some of these populations can be distinguished on the basis of differences in scale counts as well as in color pattern, more emphasis has been placed on the latter because it is usually less observably variable over wide geographic areas. Lesser variability of

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[illegible] arguments have been presented in recent years, most notably in the genus of Sceloporus occidentalis, both for and against discarding the trinomen. In recognizing subspecies in this study I am not arguing for the "reality" of these or of any other geographic races as evolutionary units. With most geographic variation being of the discordant type, it is apparent that in most cases it is the individual characters (or small groups thereof) which are undergoing selection in the evolutionary process. The systematist is thus forced to select one or more characters with which to define the geographic populations to which he gives taxonomic recognition. The subspecies is, consequently, an arbitrary entity albeit, I believe, a useful one. It is a convenient tool which allows us to locate geographically and to describe the nature of distinctive intraspecific populations in one word. This, to me, seems ample justification for its existence and continued usage.

color patterns as opposed to ventral and subcaudal numbers appears to be a common occurrence in the genus Thamnophis (Fitch, 1941; Fox, Gordon, and Fox, MS). The latter workers have shown that color pattern in individuals of T. elegans subjected to low temperatures during their embryonic development does not differ from the pattern in those animals which underwent development at normal temperatures. Ventral and subcaudal numbers of the two groups, on the other hand, are strikingly different.

Recent systematists who have worked with the garter-snakes generally fit into one of two categories: i.e., those who base taxonomic recognition of intraspecific populations primarily on color pattern (Fitch and Fox) and those who define subspecies largely on the basis of differences in the number of ventrals and subcaudals (Ailstead, Rittleman, A. G. Smith, and H. M. Smith). This dichotomy of viewpoints applies equally well to most other snake genera. A recent paper on T. sirtalis parietalis and its allies (Fitch and Maslin, 1961) in which number of ventrals and subcaudals is dismissed with two brief sentences on the general trends of clinal variation in these characters, and an earlier paper on Thamnophis marcianus (Rittleman, 1950) which recognizes two subspecies solely on the basis of meristic differences, represent the extremes of the two approaches. The fact that variation in color pattern and in meristic characters is frequently discordant makes these

differences in interpretative approach a real problem. Geographic races recognized by practitioners of the two schools of interpretation simply are not, in most cases, equivalent. Were these workers to study the same material, the range limits of the included subspecies would certainly be quite different, even if the same number of races were recognized--which is unlikely.

The chaos inherent in such a situation provides opponents of the subspecies concept with an excellent argument for discontinuing the trinomial system of nomenclature. Neither interpretative approach can be said to be the only correct one, inasmuch as the characters emphasized in each case are merely different expressions of the same genetic system. However, if the subspecies is to play a meaningful role in ophidian systematics, a uniform basis for interpretation must be established. The only alternative is to discard the trinomial system. Although a compromise of sorts might be achieved by applying subspecific names only to those populations which display concordance of color pattern and meristic characters, this occurs so infrequently that many distinctive populations would go unrecognized. Consequently I propose that in studies of geographic variation, at least in the case of the gartersnakes, meristic characters such as ventrals and subcaudals should be thoroughly investigated, carefully analyzed, and fully reported, but that the definition of geographic races be

based (when variation is discordant) on color pattern, which has been shown in several species of Thamnophis, both experimentally and in nature, to be the more observably stable character. That procedure has been followed throughout the present study.

The pitfalls inherent in an attempt to apply an hypothesis based on one species to other forms are fully recognized, but the investigations thus far which have given much attention to both types of characters (Fitch, 1941; Fox, Gordon, and Fox, MS; the present study) have found color pattern to have less observable variability. The species thus studied represent three of the four presently recognized species groups [some authors (Van Denburgh and Slevin, 1918; Smith and Hubbey, 1960) would recognize a fifth group to accommodate Thamnophis eques-trigrinus], which leads me to believe that the preceding conclusions on character variability can reasonably be extended to include the entire genus. They undoubtedly apply to a number of other snake genera as well, but each group should be evaluated independently.

The six major populations which I am recognizing herein as geographic races of Thamnophis proximus are characterized below within the framework of their formal description as subspecies.

The following key for distinguishing the subspecies of T. proximus was especially designed to be used with

living or freshly killed specimens. Inasmuch as certain colors are quickly and drastically altered by preservative, if only preserved material is available, considerable emphasis will have to be placed on "geographic probability."

Key to the subspecies of Thamnophis proximus

1. Dorsum black; vertebral stripe orange and usually narrow; dark ventrolateral stripes lacking . . . . . T. p. proximus (p. 64)

1'. Dorsum olive-grey or some shade of brown . . . 2

2(1'). Dorsum dark to very dark brown; vertebral stripe gold, not broad; dark ventrolateral stripe broad, usually 1/6 to 1/5 of a ventral scale wide; tail relatively short (mean tail length/total length in males 0.275, females 0.270); parietal spots usually chevron-shaped . . . . . T. p. alleni (p. 81)

2'(1'). Dorsum olive-grey or brown (not dark); dark ventrolateral stripe relatively narrow or absent; tail relatively long (mean tail length/total length usually exceeding 0.290 in males, 0.280 in females); parietal spots rarely chevron-shaped 3

3(2'). Vertebral stripe bright red, not broad; ventrolateral stripes narrow or lacking . . . . . T. p. rutrilineatus (p. 69)

3'(2'). Vertebral stripe orange, greyish tan, or some shade of gold 4

4(3'). Vertebral stripe greyish tan, broad; labials yellow-orange; lateral stripe narrow anteriorly, further reduced posteriorly; mean number of ventrals not exceeding 160 in males or 157 in females . . . . . T. s. rutiloris (p. 77)

4'(3'). Vertebral stripe orange or some shade of gold; greenish white or greenish yellow labials; lateral stripe not narrow, at least anteriorly; mean number of ventrals exceeding 162 in males and 158 in females . . . 5

5(4'). Vertebral stripe orange, not broad; dorsum usually olive-grey; lateral stripe frequently reduced posteriorly; narrow ventrolateral stripe frequently present . . . . . T. s. diabolicus (p. 72)

5'(4'). Vertebral stripe usually some shade of gold, broad; dorsum usually olive-brown; lateral stripe rarely reduced; ventrolateral stripe usually absent . . . . T. s. sirtalis (p. 66)

Geographic variation has already been discussed in detail, hence only those features pertinent to a formal description of the subspecies are presented below.

Accounts of Subspecies

Thamnophis proximus proximus (Say)

Tropidonotus sauritus var. fairvai Duméril, Bibron, & Duméril, 1854: 585 [by implication]

Tropidonotus sauritus var. proximus Jan, 1863: 70

Thamnophis sauritus var. proximus Duméril & Bocourt, 1870: 757

Thamnophis sauritus var. fairvai Duméril & Bocourt, 1870: 758

Thamnophis sauritus proximus Ruthven, 1908: 93

Thamnophis proximus proximus Hoseman, MS

Holotype. The information presented for the species (p. 16) applies here. Although the holotype is thought to be lost, a neotype has not been designated because the original description (Say, 1823) and the type locality are adequate to associate the name with a specific population.

Definition. A subspecies of Thamnophis proximus characterized by a black dorsum, a narrow orange vertebral stripe, and lack of a dark ventrolateral stripe.

Range. This race ranges from Indiana and southern Wisconsin south in the Mississippi Valley to, but not including, southern Louisiana, west through southern Iowa and extreme eastern Nebraska to central Kansas, central Oklahoma, and eastern Texas (exclusive of the coast).

Description. Inasmuch as the holotype is not available, the following description is based on UF 12100-1,

an adult male collected 6.5 miles S.Jeffersville, Chase County, Kansas, by William E. Duellman.

Scutellation is as follows: oculars 1+3, temporals 1+2, supralabials 8, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 157, subcaudals 108. Body length is 394 mm., tail length 156, tail length/total length ratio 0.497.

The dorsum is black over most of the body, becoming a very dark brown posteriorly, dark brown below the lateral stripe.[1] The vertebral stripe is pale orange (Maerz & Paul 1147), the lateral stripe light yellow. The venter is yellowish green with a pale orange tinge along the lateral margin of each scute, the dark ventrolateral stripe lacking entirely. The pale yellow postocular spot occupies all of the lower and anterior half of the middle postocular; the fused parietal spots are moderately prominent and bright.

Discussion. Meristic and proportional characteristics of this subspecies may be summarized as follows: 2 to 4 postoculars; 1+1 to 2+3 temporals; 7 to 9 supralabials; 8 to 11 infralabials; 1 to 3 intergenials; 17-19-15 to 21-19-17 dorsal scale rows; males 151-173, females 154-176 ventrals; males 99-131, females 90-120 subcaudals. Males range from 122 to 342.5 mm. in body length, 174 to

[1]All color descriptions in this study are based on freshly killed, freshly shed specimens, unless otherwise stated.

755 mm. in total length; adult tail length/total length ratio 0.284 to 0.333. Females range from 120.5 to 690 mm. in body length, 177.5 to 956 mm. in total length; adult tail length/total length ratio 0.267 to 0.336.

Intergrades between T. s. proximus and either T. s. rubrilineatus or T. s. diabolicus have not been seen in life, but from the little that can be ascertained from preserved specimens about the distribution of brown or black dorsa where the ranges of the subspecies would be expected to meet, it appears that the black T. s. proximus intergrades with one brown race (diabolicus) over a broad zone in southwestern Kansas, western Oklahoma, and the eastern part of the Texas panhandle, with still another brown form (rubrilineatus x diabolicus intergrades) in north-central Texas, and finally with T. s. rubrilineatus in east-central Texas. Intergradation between T. s. proximus and T. s. orarius is discussed under the latter form.

Thamnophis proximus orarius,[1] new subspecies

Holotype. TU 11764, an adult female from Lapeyrouse, Jefferson Parish, Louisiana, collected 23 February 1950.

Definition. A subspecies of Thamnophis proximus characterized by an olive-brown dorsum, a broad gold vertebral stripe, and lack of a dark ventrolateral stripe.

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[1]refers to the fact that this race lives along the coast.

Range. This subspecies ranges from Cat Island and southwestern Hancock County, Mississippi, through southern St. Tammany Parish, Louisiana, south and west along the Gulf Coast, probably as far as northern Tamaulipas.

Description of holotype. Scutellation is as follows: oculars 1+3, temporals 1+2, supralabials 8, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 169, subcaudals 106. Body length is 463 mm., tail length 200 mm., tail length/total length ratio 0.30+.

The following color description is based on UF 12165, an adult female collected 3 miles E Boutte, St. Charles Parish (approximately 7½ miles W Waggaman) by Harold J. Dundee: dorsum olive-brown (Maerz & Paul 15H9), greyish brown below the lateral stripe (15L4); vertebral stripe gold (13L4), broad; lateral stripe yellow (10L1); venter pale green medially (16L3), lateral margins orange (11L6); dark ventrolateral stripe lacking entirely; chin shields white; supralabials pale yellowish green, anterior three tannish. The pale yellow postocular spot occupies all of the lower and middle postoculars and the leading edge of the upper one; the fused parietal spots are moderately prominent and bright.

Discussion. Meristic and proportional characteristics of this subspecies may be summarized as follows: 2 to 4 postoculars; 1+1 to 2+3 temporals; 7 to 8 supralabials; 8 to 11 infralabials; 1 to 4 intergenials; 17-19-17 to 21-21-17

dorsal scale rows; males 161-151, females 159-177 ventrals; males 97-127, females 97-144 subcaudals. Males range from 139 to 553 mm. in body length, 243 to 704 mm. in total length, adult tail length/total length ratio 0.280 to 0.346. Females range from 170 to 900 mm. in body length, 241.5 to 1434+ mm. in total length, adult tail length/total length ratio 0.273 to 0.349.

I have seen living proximus x ornatus intergrades from Harris County, Texas, and St. James and northern St. Charles Parishes, Louisiana. All have vertebral stripes more or less typical of ornatus. The St. Charles Parish specimens (UF 14161 from 1 mile N St. Rose) range from fairly typical brown-dorsum ornatus to individuals which are almost black. The keels of the dorsal scales are brown, but varying amounts of the remaining area of each scale are black. Specimens from Refugio, San Patricio, and Victoria Counties, Texas, also have varying amounts of black pigment on essentially brown scales, but these represent variations from a wholly brown dorsum rather than intergrades inasmuch as the black-dorsum proximus does not appear to range that far west inland. Most of the St. James Parish individuals are entirely black.

The situation in Harris County is not clear. Two adults (UF 12203) from Channelview at the head of Galveston Bay have entirely black dorsa and gold vertebral stripes, but a subadult from the same locality appears to be an

orarius. The situation is further complicated by five typical orarius from 9 miles s Tomball in northwestern Harris County, this locality being several miles farther inland than Channelview where intergrades occur. Typical proximus are found in Liberty County, the next county to the east.

No live intergrades with other subspecies have been seen, but I suspect that all of inland southern Texas is an area of intergradation between this race, T. s. rubrilineatus, and T. s. sirtalicus. Specimens from south-central Tamaulipas appear to be intergrades between orarius and pallidus, tetrataenia and parietalis, or all three forms.

Thamnophis sirtalis rubrilineatus,[1] new subspecies

Holotype. UF 12166-3, an adult male from the State Fish Hatchery, 3.2 miles NW Ingram, Kerr County, Texas, collected 26 June 1960 by H. J. Fouquette, Jr., and Douglas A. Rossman.

Definition. A subspecies of Thamnophis sirtalis characterized by an olive-brown to olive-grey dorsum, a bright red vertebral stripe, and a narrow dark ventrolateral stripe or none at all.

Range. This subspecies is distributed throughout the Edwards Plateau region of central Texas and northward an undetermined distance (probably not much farther north than San Angelo or Waco).

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[1] Refers to the presence of a bright red vertebral stripe in members of this subspecies.

Description of holotype. Scutellation is as follows: oculars 1+2, temporals 1+2, supralabials 8, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 170, subcaudals 107. Body length is 353 mm., tail length 141 mm., tail length/total length ratio 0.285.

The dorsum is olive-brown (Maerz & Paul 15D5), a lighter shade of brown below the lateral stripe (15L2). The vertebral stripe is red (4L14) on the posterior three-fourths of the body, orange (9L11) on the neck; the lateral stripe is light yellow (10L1). The venter is pale green (16L4), the posterior edge of each ventral scute cream yellow; the dark ventrolateral stripe is lacking. The chin shields are white, the supralabials pale greenish white. The pale yellow postocular spot occupies all of the lower and the leading edge of the middle postocular; the fused parietal spots are moderately prominent and bright.

Discussion. Meristic and proportional characteristics of this subspecies may be summarized as follows: 2 to 4 postoculars; 1+1 to 2+3 temporals; 7 to 9 supralabials; 9 to 11 infralabials; 1 to 4 intergenials; 19-19-15 to 19-19-18 dorsal scale rows; males 163-174, females 150-175 ventrals; males 96-119, females 93-116 subcaudals. Males range from 243 to 493 mm. in body length, 319 to 711 mm. in total length; adult tail length/total length ratio 0.280 to 0.342. Females range from 169 to 725 mm. in body length, 234 to 994 mm. in total length; adult tail length/total length ratio 0.266 to 0.340.

Fourteen individuals out of a series of fifteen from 8 miles S Oak Hill, Hays County, Texas, have the usual bright red vertebral stripe. The stripe on the other specimen (UF 12204-1) is orange throughout the length of the body. A series of five snakes from Fern Bank Springs, Hays County, all have the red stripe as does another series of five from a few miles NW Austin, Travis County. Only red stripes are present in seven individuals from scattered localities in Blanco County. Seven snakes collected at the type locality in Kerr County have red stripes (others seen at this locality, but not collected, agree in stripe color). One of two specimens from the Devil's River in northern Val Verde County agrees well with the above; in the other (UF 12189-2), the vertebral stripe is orange (Maerz & Paul 3B12) on the anterior half of the body. The stripe thereafter is bright red (3R12). Of a series of 17 animals from 6.5 miles S Colorado City, Mitchell County, 14 have orange vertebral stripes, 1 has a reddish orange stripe, and the remaining 2 have red stripes. This series apparently represents a population of rubriliratum x diabolicus intergrades but one which receives a preponderance of genetic influence from diabolicus.

A red-striped individual from the edge of the Balcones Escarpment at New Braunfels, Comal County, is reported by Stone (1903). Gloyd (1935) describes a red-striped specimen from near Floresville, Wilson County. This

locality is some distance from the Escarpment and the animals there may be intergrades rather than typical rubrilineatus. Strecker (1908) indicates that the ribbon-snakes in Coleman County usually have a red vertebral stripe. One rather puzzling record of a red-striped snake is that of Brown (1901) who reports one from Pecos, Reeves County, which is over 100 miles west of the westernmost verified localities for red-striped individuals. All other records from trans-Pecos Texas are of animals with an orange vertebral stripe. Unless this represents the aberrant individual which resembles one subspecies while occurring within the range of another race, I am reluctant to accept the accuracy of the locality data until additional specimens are available.

Thamnophis proximus diabolicus,[1] new subspecies

Holotype. UF 12210, a large adult female from the Rio Nadadores, 8 miles n Nadadores, Coahuila, Mexico, collected 3 August 1960 by Roger Conant.

Definition. A subspecies of Thamnophis proximus characterized by an olive-grey to olive-brown dorsum, an orange vertebral stripe, a narrow dark ventrolateral stripe, and frequent reduction in the width of the lateral

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[1] In allusion to another horned inhabitant of hot places. The ribbonsnake's "horns" however are strictly pictorial, being represented by the forked condition of the parietal spots, a condition found in many individuals of this area-dwelling race.

stripe on the posterior portion of the body in the southern part of the range.

Range. This subspecies ranges from west-central Tamaulipas, Nuevo Leon, and eastern Coahuila northnortheast through the Pecos Valley of Texas and New Mexico and, possibly, the Staked Plains of western Texas and adjacent New Mexico to extreme southeastern Colorado (Baca County). Isolated populations may exist in the Rio Grande Valley in western New Mexico (see Discussion).

Description of Holotype. Scutellation is as follows: oculars 1+3, temporals 1+3, supralabials 8, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 166, subcaudals 99. Body length is 771 mm., tail length 309 mm., tail length/total length ratio 0.286.

The color pattern is as follows: dorsum olive-grey; vertebral stripe yellowish orange immediately behind the head, a bright orange thereafter, not broad; lateral stripe reduced in width posteriorly; venter greyish white medially, pale orange marginally; dark ventrolateral stripe occupies 1/10 the width of a ventral scute on each side; chin shields white; supralabials pale greenish white. The light postocular spot is confined to the lower postocular and is not brightly colored; the fused parietal spots are prominent, bright yellow in color, and broadly margined with black; a black postorbital vitta is lacking.

Because a color atlas was not available at the time the above color notes were made, the following supplementary

notes are presented for a subadult female (UF 12417-1) collected in Huisteco Canyon, near Santa Catarina, Nuevo Leon, by H. J. Poinsett, Jr., and Douglas A. Rossman: dorsum olive-brown (Ridgway 43J7); vertebral stripe bright orange (13A10); lateral stripe bright yellow (13F1); venter pale yellow-green (15A3).

Discussion. Meristic and proportional characteristics of this race may be summarized as follows: 3 to 4 postoculars, 1+1 to 2+3 temporals; 8 to 9 supralabials; 9 to 11 infralabials; 1 to 4 intergonials; 19-19-15 to 21-19-17 dorsal scale rows; males 161-171½, females 157-169 ventrals; males 93-114, females 57-103 subcaudals. Males range from 165 to 415 mm. in body length, 459 to 593 mm. in total length; adult tail length/total length ratio 0.405 to 0.307. Females range from 179 to 771 mm. in body length, 446 to 1050 mm. in total length; adult tail length/total length ratio 0.403 to 0.304.

The populations in Nuevo Leon, Coahuila, trans-Pecos Texas, and southern New Mexico are typical of the subspecies as here described. A single specimen (UMMZ 80940) from Union County in extreme northeastern New Mexico also seems to belong with this group. KU 49535 from Hartley County, Texas, and USN 11869-873 from Baca County, Colorado, are apparently representatives of populations of *disparilicus*, although the dorsum may be somewhat darker than is usual for this race. The northeastern New Mexico and Texas

individuals were collected on tributaries of the Canadian River, the Colorado series from a tributary of the Cimarron River. These are both eastward-flowing streams, yet the snakes show much less affinity to the populations in more eastern parts of the Canadian and Cimarron drainages than they do to the animals of the Pecos River drainage. Since ribbonsnakes in arid regions are generally restricted to the immediate vicinity of permanent springs and watercourses, these northern populations of Thamnophis are probably fairly effectively isolated from those in the Pecos drainage and represent relicts which were part of a continuously distributed population at a time when conditions were more mesic.

A similar pattern of disjunct distribution in this same general area occurs in Thamnophis sirtalis (Fitch and Maslin, 1961). That species has an isolated population in the Rio Grande Valley of New Mexico, and it is possible that T. proximus may have one there also. There are several old records for this area, but there is some doubt as to their validity. Baird and Girard (1853) list two proximus from New Mexico at Sabinal and Medina, and discuss in the text some specimens from the Rio Grande Valley. Inasmuch as none of the other specimens listed are from localities anywhere near the Rio Grande, I assume that the writers are referring to the New Mexico specimens. There is a Sabinal on the west side of the river in northern

Socorro County, but I have been unable to locate a Medina anywhere in New Mexico; and F. A. Dehlbach, who is studying the herpetofauna of the state, has informed me that he knows of none. Mr. Dehlbach also thinks there is a possibility that the snakes may actually have been collected in Texas at Sabinal, Uvalde County, and Medina, Bandera County, rather than in New Mexico. The specimens themselves are apparently no longer extant. Two individuals (USNM 63751) from "east of Albuquerque" may be from the Pecos drainage inasmuch as their collector, an entomologist, donated to the museum several species collected at stations from Pecos, San Miguel County, west to Albuquerque (F. A. Dehlbach, pers. comm.). Thus there is no conclusive evidence that the western ribbonsnake occurs in the Rio Grande Valley, but the distribution pattern of T. sirtalis dorsalis (incorrectly referred to as T. s. ornata by Fitch and Maslin, 1961) with its isolated populations in the Canadian and Pecos drainages as well as along the Rio Grande, leads me to think that it may do so.

Specimens from the eastern edge of the Staked Plains appear to be intergrades between diabolicus and proximus in the north, diabolicus and rubrilineatus in the south. North-central Texas populations may be intermediate between all three races.

Intergradation between diabolicus, rubrilineatus, and ararius, in varying combinations, apparently occurs throughout most of inland southern Texas. Individuals from the

eastern foothills of the Sierra Madre Oriental in west-central Tamaulipas (as far south as Ciudad Victoria) are here considered to represent the southernmost population of diabolicus, but living material may show them to be diabolicus x orarius intergrades. Possible intergrades between diabolicus and rutiloris are discussed under the latter subspecies.

Thamnophis proximus rutiloris (Cope)

Thamnophis sauritus rutiloris Smith, 1938: 5

Thamnophis sauritus chalceus Dunn, 1940: 192

Thamnophis proximus rutiloris Rossman, MS

Holotype. USNM 13906, an adult female from Cozumel Island, Quintana Roo, Mexico, collected 23-27 January 1885 by personnel of the U.S. Fish Commission vessel Albatross (Cochran, 1961).

Range. This race extends from extreme southern Tamaulipas south along the coastal plain, eastern rim of the Sierra Madre Oriental, and Central American highlands to Cartago, Costa Rica. It occurs in the Pacific lowlands only at the Istmus of Tehuantepec and in central Guerrero. There are no records for the highlands of Guatemala.

Description of holotype. Scutellation is as follows: oculars 1+3, temporals 1+1,2 (the left anterior temporal is fragmented anteriorly), supralabials 8, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 147, subcaudals 97 (tip damaged but apparently complete). In

the original description Cope reports 92 subcaudals. Body length is 540 mm., tail length 415 mm., tail length/total length ratio 0.493. Cope (1889) records a body length of 533 mm. and a tail length of 414 mm. This discrepancy in body measurements is undoubtedly due to shrinkage of the holotype during 75 years storage in preservative.

The holotype is described (Cope, 1889) as having a brownish-olive dorsum; vertebral stripe existing only as a faint trace; lateral stripe pale olive; venter pale olive; supralabials, infralabials, and first 3 ventrals reddish-orange or salmon; a pair of light parietal spots present. It is not clear whether this description was of the living animal; hence a color description is here given of UF 12215, an adult female collected 13 miles NW Veracruz, Veracruz, by A. J. Fouquette, Jr., and Douglas A. Rossman: dorsum olive-tan in life, somewhat lighter below the lateral stripe; vertebral stripe greyish tan, broad; lateral stripe pale yellow, narrow, and slightly reduced in width on the posterior part of the body; venter pale yellow at neck becoming pale green posteriorly; dark ventrolateral stripe narrow, occupying 1/10 the width of a ventral on each side; chin shields and lower margin of infralabials white; supralabials and upper margin of infralabials bright yellow (ten other live rutiloris have yellow-orange labials). The light postocular spot occupies the lower and leading edge of the middle postocular but is not brightly colored;

the fused parietal spots are prominent, bright yellow, and broadly margined with black. The black postorbital vitta is narrow, irregular, and confined to the temporals.

Discussion. Meristic and proportional characteristics of T. s. rutiloris may be summarized as follows: 2 to 5 postoculars; 1+1 to 2+3 temporals; 7 to 9 supralabials; 8 to 11 infralabials; 1 to 6 intergenials; 17-16-17 to 21-19-17 dorsal scale rows; males 142-164, females 141-160 ventrals; males 91-104, females 82-98 subcaudals. Males range from 157.5 to 445 mm. in body length, 222 to 543 mm. in total length; adult tail length/total length ratio 0.286 to 0.307. Females range from 153 to 590 mm. in body length, 210.5 to 776 mm. in total length; adult tail length/total length ratio is 0.275 to 0.306.

Three specimens from between El Limon and Chanal in extreme southwestern Tamaulipas apparently represent intergrades between rutiloris and diabolicus. The two females (UMMZ 101222, 101903) have the broad vertebral stripe characteristic of rutiloris, but in life it almost surely was of some color other than tan (presumably orange). The ventral counts (158, 160) are well within the normal range of variation for Mexican diabolicus. UMMZ 110315, a male, has a vertebral stripe which apparently was tan and 152 ventrals, the former characteristic of rutiloris, the latter of diabolicus.

A series of snakes (CNAH 114532-560, UMMZ 102892-894, UMMZ 103926-928, CNAH 105305) from the Sierra de Tamaulipas

on the Tropic of Cancer appears to combine the color pattern of *ornatus* (or *ornatus* × *cinctulatus* intergrades) with ventral counts which are much closer to those of *rutiloris*. Women from the immediate vicinity of Ciudad Mante appear to have the color pattern of *rutiloris*, but the males have a rather high ventral count (the females have a ventral count comparable to those of female *rutiloris* 400 miles to the south). The populations in eastern San Luis Potosí and near Tampico are considered to be *rutiloris*.

The only available representative of the possibly relict population in coastal Guerrero (UF 14413) has a vertebral stripe which is not broad and definitely was not tan in life, but rather seems to have been a pale yellow. Furthermore, the lateral stripe is largely confined to row 3 as in *T. s. albinus*. On the other hand, the specimen agrees with lowland *rutiloris* in scutellation, color of dorsum, width of ventrolateral stripe, and proportional muscle length. Until such time as additional material (particularly live specimens) becomes available to confirm or deny the distinctiveness of this population, it would be pointless to give it taxonomic recognition.

A specimen (MVZ 80046) from the mountains of south-central San Luis Potosí near Zaragoza (km. 44, Potosí-Río Verde Railroad) is rather far removed from the range of *rutiloris* as presently understood, and this record needs substantiation.

Thamnophis proximus alpinus,[1] new subspecies

Holotype. UF 12216, an adult male from the trout hatchery at San Cristobal Las Casas, Chiapas, Mexico, collected 1 August 1960 by R. J. Fouquette, Jr., and Douglas A. Rossman.

Range. This form is found in the Chiapas highlands from San Cristobal Las Casas to Comitan at elevations above 5000 feet.

Description of holotype. Scutellation is as follows: oculars 1+3, temporals 1+2 (the anterior temporal is fragmented anteriorly on both sides of the head), supralabials 8, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 163, subcaudal series and tail incomplete. Body length is 499 mm.

The dorsum is dark brown (Maerz & Paul 3L12), olive-brown below the lateral stripe (15J10). The vertebral stripe is gold (12A6) and not broad; the lateral stripe is light yellow (10A1) overlain with brown pigment, narrow, and present only on row 3 on the posterior part of the body. The venter is pale green (17L4), pale yellow at the neck; the dark ventrolateral stripe is brown, 1/4 the width of a ventral scute on each side (on the tail it covers the entire surface of the subcaudals). The chin shields are white, irregularly spotted with pale orange; the supralabials and

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[1]Refers to the high altitudes at which this subspecies lives.

infralabials are pale yellow-orange, but on the supralabials there is much brown pigment overlying the yellow-orange (the anterior 3 plates are completely overlain; there are varying amounts, irregularly distributed, on the posterior 5). The light postocular spot occupies all of the lower and the anterior part of the middle postocular, and is overlain with brown pigment; the fused, chevron-shaped parietal spots are prominent and pale yellow, overlain with brown pigment.

Discussion. Meristic and proportional characteristics of this subspecies may be summarized as follows: 2 to 4 postoculars; 1+1 to 2+3 temporals; 7 to 9 supralabials; 9 to 11 infralabials; 2 to 5 intergenials; 19-19-17 to 23-19-17 dorsal scale rows; males 157-165, females 153-163 ventrals; males 99-104, females 86-99 subcaudals. Males range from 175 to 499 mm. in body length, 241.5 to 644 mm. in total length; adult tail length/total length ratio 0.288 to 0.269. Females range from 141.5 to 543 mm. in body length, 194 to 722 mm. in total length; adult tail length/total length ratio 0.232 to 0.263.

I have not seen intergrades between alminus and rutiloris, but they might be expected to occur at lower elevations on the northern and western slopes of the Chiapas highlands. In supralabial color and lateral stripe width alminus demonstrates its relationship to the widespread rutiloris. The darker color of the dorsum in alminus, the

reduction in width of its vertebral stripe, and the overlaying of its light areas (such as the dorsal stripes) with dark pigment appear to be adaptations to reduce reflection and increase absorption of solar radiation in an environment in which the activity of ectotherms is severely restricted by the low temperatures.

The frequent occurrence of such scutellation variations as 3 intergenials and fragmentation of the anterior temporal may have been the result of increase in variability of scale characters as a result of either exposure of the mother to low temperatures during the gestation period (as demonstrated for Thamnophis elegans by Fox, 1948) or the effects of genetic drift on a normally rare variation in an essentially isolated population.

Evolutionary Trends

With the exception of alpinus which is even now at least semi-isolated at high elevations in the Chiapus highlands, the manner in which the geographic races of Thamnophin sirtalus underwent the isolation presumably necessary for their differentiation is not known, although on the basis of their present distribution it would appear that some ecological factors were, and for that matter still are, involved. Setting aside alpinus which has already been discussed, we find that: rutiloris is confined to the moist tropical tropics; obscurus occurs almost exclusively in high, arid regions; sumichrasti is found chiefly on

the Edwards Plateau of central Texas; *cervinus* is generally limited to the Gulf Coast of Louisiana and Texas; and *proximus* is distributed widely in that part of the interior of central United States in which the average precipitation exceeds 30 inches annually.

This distribution suggests that the features diagnostic of each of these major populations may have become stabilized in a particular environment as a result of differential selection. Characteristics which facilitate, or at least do not hamper, survival in a particular environment would tend to be positively selected. This seems a reasonable if somewhat obvious explanation, but it requires cautious application. *T. s. diabolicus* occurs almost entirely in arid regions, which might lead one to suppose that its characteristics reflect adaptation to life in an arid environment. Closer examination reveals that the ribbonsnake is not actually adapted to these arid conditions but occupies a restricted niche, persisting in the limited mesic situations available in the immediate vicinity of permanent water. Thus, small disjunct populations characterize much of its present distribution, and there is reason to believe that *diabolicus* was once continuously distributed when the region in which it now occurs was much more mesic.

The black dorsum of the nominate race (as well as the narrowness of its vertebral stripe) may be an adaptation for decreased reflection of solar radiation in the cooler,

northern part of the range of T. proximus where the ability to absorb and retain solar heat would be an asset. The fact that the black race also occurs in south-central United States where such an adaptation would seem to have little present-day value may indicate that T. s. proximus originally evolved in the latter area during a glacial advance, when conditions would have been much cooler, and has since extended its range northward.

Natural History

A brief summary of our knowledge of the ecology of T. proximus is presented below. No claim is made as to its completeness, and many aspects are treated in much greater detail elsewhere (Tinkle, 1957, has produced the most comprehensive study to date).

Habitat

My personal experience has been the proximus is rather closely confined throughout its range to the vicinity of permanent or semipermanent bodies of water, either running or standing, and most literature accounts substantiate this observation. Neill and Allen (1959), however, collected a large adult beneath a log in a high, dry savanna in British Honduras. Open grassy situations seem to be preferred, but I have also found the species in wet woodlands, at a desert waterhole, and in rush-lined ponds; and Ruthven (1908) reports the occurrence of the ribbonsnake in brackish mangrove swamp at Progreso, Yucatan. Few

authors have referred to the semiarboreal habits of this species. Specimens of proximus have been observed in bushes in British Honduras (Dumeril and Bocourt, 1870), Kansas (Lloyd, 1940), and Nebraska (Hudson, 1942), and I have collected them several feet above the water (one over 6 feet up) in reeds in Chiapas and San Luis Potosí.

Food

The diet of the western ribbonsnake is chiefly confined to amphibians and their larvae, and to fishes. Species that are definitely known to have been eaten by Thamnophis proximus (other than under laboratory conditions) are listed in Table 3. Taylor (1892) and Fouquette (1954) have also recorded insects in the diet of the western ribbonsnake, but it is likely that these were the result of secondary ingestion. Wright and Wright (1957) indicate that there is an account in the literature of T. proximus eating mice. I believe that they may have been referring to Trowbridge (1937), who reports finding a proximus in a mouse nest in a log. The snake contained Sorex ribidus, however, not mice. Endothermic vertebrates, lizards, earthworms, and other invertebrates, all of which are readily eaten by one or more species of gartersnake are apparently not voluntarily ingested by T. proximus. Moreover, while newly transformed toads are readily accepted by captive ribbonsnakes, adult bufo are almost always refused. It may be possible that members of the sauritus group are

Table 8.--Food of *Taumichthys proximus*

Species	Source
Anurans	
Pelobates hemiphrus	Fouquette, 1954
Bufo woodhousei	Fouquette, 1954
Acris crepitans	Fouquette, 1954
Acris gryllus	Boyer and Holmes, 1934
Hyla crucifer	Fouquette, 1954
Hyla versicolor	Lloyd, 1926; Fouquette, 1954
Rana pipiens	A. J. Fouquette, Jr., pers. comm.
Pseudacris clarki	Fouquette, 1954
Pseudacris streckeri	Fouquette, 1954
Pseudacris triseriata	Lloyd, 1926; Fouquette, 1954
Rana catesbeiana	Fouquette, 1954
Rana pipiens	Fouquette, 1954
Rana sphenocephala	Trowbridge, 1937; Clark 1949; Fouquette, 1954
Scaphiopus holbrooki	personal observation
Scaphiopus couchi	Wright and Wright, 1957
Scaphiopus multiplicatus	personal observation
Microhyla olivacea (larvae only)	Fouquette, 1954
Salamanders	
Aneides hardyi	Fouquette, 1954
Plethodon glutinosus	C. A. Myers, pers. comm.
Fishes	
Notropis shumardi	Ayers, 1957
Dorosoma cepedianum	Fouquette, 1954
Lepomis megalotis	Fouquette, 1954
Marcetinus symmetricus	Fouquette, 1954

not as well adapted physiologically as other garternakes to tolerate the toxic parotoid secretions of adult toads.

When food is readily available, a ribbonsnake may continue feeding until it is interrupted or there is no more food. Loughlin (1959) reports that a single T. proximus contained 64 metamorphosing toads of an unidentified species; and Klein (1949) observes that ribbonsnakes (as well as several species of watersnake) feeding on aggregations of fish, tadpoles, and frogs in pools left by a drop in water level of the San Antonio River, gorged themselves to the point that many of the snakes, especially the juveniles, ate themselves to death.

Ribbonsnakes are as active at night as during the day, at least where nocturnal temperatures permit, and apparently feed as readily at one time as the other. Near Ciudad Mante in Tamaulipas, M. J. Fouquette, Jr. (pers. comm.) watched a T. proximus stalk a calling Smilisca baudini. When the frog's vocal sacs moved, the snake moved closer, stopping each time the frog stopped calling.

Reproduction

Tinkle (1957) has found that ribbonsnakes in southeastern Louisiana reach sexual maturity in approximately 2 years and at a minimum body length of 405 mm. in females and 410 mm. in males. Cloyd (1940) reports that a Kansas female with a body length of 435 mm. bore young, and Carpenter (1952) notes the same thing for a female from

Oklahoma with a body length of 400 mm. Clark (1949) records a brood from a 420-mm female from northern Louisiana. If he is referring to total length and if the animal was a complete tail, its body length is probably between 390 and 300 mm. The smallest gravid females which I have examined measure 355 (British Honduras), 385 (Veracruz), 390 (Veracruz), 442 (southeastern Texas), 450.5 (Veracruz), and 454 (San Luis Potosí) mm. in body length. The fact that five of these six animals are from tropical America may indicate that sexual maturity is achieved at a smaller size in that region. Extrapolating from Finkle's data we can estimate that males in Mexico and Central America probably mature at a body length of 330 mm. or slightly longer.

Mating apparently takes place soon after the spring emergence (in areas where there is winter inactivity). Carpenter (1958), Neill and Allen (1959), and Finkle (1957) all having found gravid females as early as April. The young are usually born in late July or early August, but dates range from 10 July (Finkle, 1957) through 14 September (Carpenter, 1958). Brood size ranges from 4 (Carpenter, 1958) to 27 (Alcin, 1949), the mean for 34 broods being 14.8 individuals. The size of the brood tends to increase with the size of the female. Available data on body length of newly born T. *erythrus* are summarized in Table 9. There is much variation between broods in size of individuals

Table 3.--Body length of newly born Thamnophis sirtalis

Locality	n	M	R
St. Charles Parish, La.[a]	22	204.6	187 -220
St. Charles Parish, La.[b]	3♂♂	201.7	198 -214
	3♀♀	198.0	190.5-206
	2♂♂	177.8	176.5-179
	2♀♀	173.5	170 -176.5
Alexander Co., Illinois[c]	8	157.3	151 -164
Southern Oklahoma[d]	5♂♂	206	194 -225
	7♀♀	201	199 -204
	4♂♂	170	165 -174
	7♂♂	159	156 -160
	2♀♀	152	148 -156
Eastern San Luis Potosi[b]	1♂	166	
	4♀♀	164	164 -168

n = number of individuals; M = mean; R = range

[a]Data from Tinkle, 1957
[b]Personal observation
[c]Data from H. J. Rossman, 1958
[d]Data from Carpenter, 1958

at birth, but if such size varies geographically it is not readily apparent. Males average larger than females at birth, but smaller as adults.

Parasites

Harwood (1932) reports finding the helminths Guyanian vellardi and Rallocephalus pulaterodactis in the lungs and stomach, respectively, of Thamnophis proximus. In examining MCZ 53912, an adult female proximus from near Merida, Yucatan, I discovered a small tick embedded on the left side of the head at the junction of the anterior temporal, lower postocular, and sixth supralabial. Dr. George Amstos has identified it as a nymphal stage of the genus Ixodes (species undetermined).

Thamnophis sauritus (Linnaeus)

Coluber sauritus Linnaeus, 1766: 389

Natrix sauritus Merrem, 1820: 122

Tropidonotus sauritus Boie, 1827: 535

Leptophis sauritus Holbrook, 1842: 21

Thamnophis sauritus Fitzinger, 1843: 26 [by implication]

Eutainia sauritus Baird & Girard, 1853: 24

Eutaenia packardii Kennicott, 1859: 98

Eutaenia sauritus Kennicott, 1859: 98 [by implication]

Pramnesticus chalcaeus Cope, 1860: 558

Tropidonotus (Eutainia) sauritus Jan, 1863: 69

Tropidonotus sauritus Garman, 1883: 23

Eutaenia packeni Davis and Rice, 1883: 39

Thamnophis packenii Loennberg, 1894: 349

Thamnophis sauritus Stone, 1906: 164

Thamnophis packeni Deckert, 1918: 31

Material

Since the holotype (collected in "Carolina") is presumed to be lost, Schmidt and Conant (1956-57) have designated as neotype, CNHM 73119, an adult female from 15 miles NNW Charleston, Berkeley County, South Carolina, collected 20 July 1953 by John Quinby.

Definition

A moderately large, long-tailed member of the genus Thamnophis characterized by: 19-19-17 dorsal scale rows; a single preocular; 7 or 8 supralabials, the third and fourth or fourth and fifth, respectively, entering the orbit; 143 to 177 ventrals; 94 to 136 subcaudals; lateral stripe on dorsal scale rows 3 and 4 (row 2 is occasionally involved); labials and ventrals without black markings; dark ventrolateral stripe always present and broad; parietal spots frequently lacking, when present they are small, and rarely in contact or brightly colored; hemipenes short, extending to the eighth subcaudal when inverted; maxillary teeth numerous, usually 23 to 28 in number.

Range

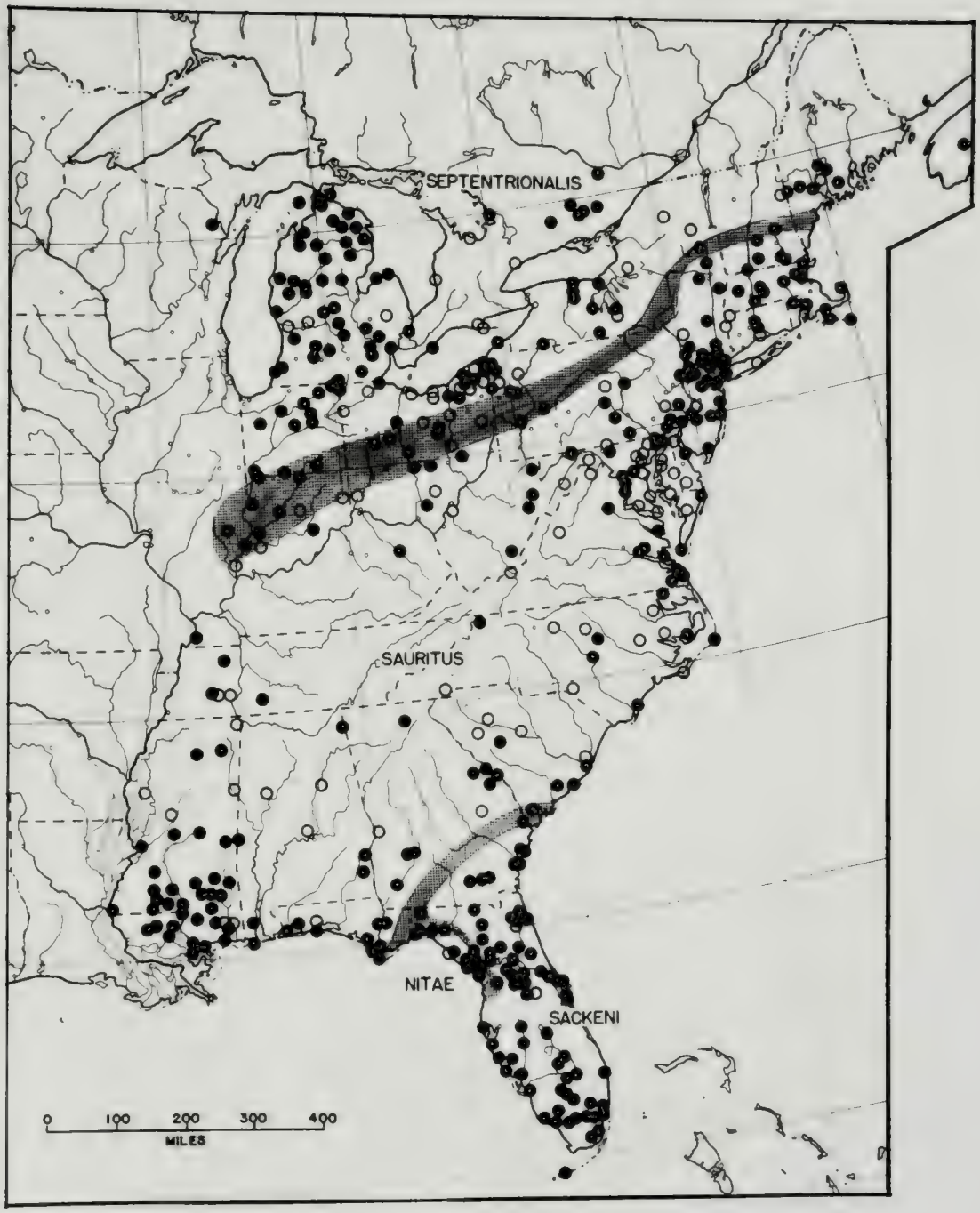
This species ranges from Michigan, southern Ontario, and southern Maine, southward east of the Mississippi River to the northern side of Lake Pontchartrain in Louisiana, and to the Florida Keys (Figure 8). There is an isolated colony in central Nova Scotia, and there may be one in northern Wisconsin. The species apparently is rare in much of the interior of eastern United States.

Variation

Sexual Dimorphism

Thamnophis sauritus shows sexual dimorphism in the same characters as does T. sirtalis, and to about the same

United States and Canada. Solid dots represent specimens examined; open circles are literature records. Stippled areas represent the probable zones of intergradation between subspecies.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MILES

degree (see Table 3). In populations for which at least five snakes of each sex are available, the difference in mean number of ventrals ranges from 0.6 scales in favor of the females (Charleston County, South Carolina) to 5.7 in favor of the males. The greatest dimorphism occurs in the western half of peninsular Florida; in other areas the degree of dimorphism does not appear to vary geographically. The populations from which at least 15 adults of each sex are available are compared in Table 10.

Sexual dimorphism in subcaudal number also agrees well with that exhibited by F. proximus (Table 5), but does not vary as widely. There are no samples with at least five of each sex in which males have fewer subcaudals than the females. The mean differences range from 3.4 (south-central Mississippi) to 10.3 (southeastern Pennsylvania). There does not appear to be any geographic variation in this character. Those populations for which at least ten adults of each sex are available are compared in Table 11.

Females average longer than the males but have a proportionally shorter tail. The largest female examined (UF 12120 from Dade County, Florida) has a body length of 670 mm., a tail length of 345 mm. The largest male (UMMZ 106313) is also from Dade County and has a body 537 mm. long and a tail 283 mm. long. Wright and Wright (1957) cite a New Jersey male with a total length of 844 mm.

The mean differences in adult tail length/total length ratio ranges from 0.007 to 0.014 (in all populations

Table 10.--Sexual dimorphism in ventrals in [illegible]

Population	Males		Difference		Females	
	N	M	Dif	Dif	N	M
Southeastern Florida	40	164.7±0.83	5.4	3.31±0.13	47	159.3±0.43
North-central Florida	15	157.8±0.92	3.6	2.31±0.29	25	154.2±0.74
Southern Michigan	16	163.1±0.93	2.4	1.4±0.97	25	160.7±0.63

N = number of individuals; M = mean; Dif. = difference between means; CD = coefficient of divergence expressed as a percent

Table 11.--Sexual dimorphism in subcaudals in [illegible]

Population	Male		Difference		Female	
	N	M	Dif	Dif%	N	M
Southwestern Florida	11	120.2±1.54	7.9	6.05±0.39	16	112.4±0.96
North-central Florida	13	143.3±1.43	7.7	6.45±0.39	13	115.6±1.26
Eastern Michigan	10	108.3±1.16	5.3	5.02±0.38	16	[illegible]±1.09

N = number of individuals; M = mean; Dif = difference between means; Dif% = coefficient of divergence expressed as a percent

males have a proportionally longer tail than the females). Mean tail length/total length values range from 0.313 to 0.373 in males, 0.299 to 0.350 in females.

Although females have proportionally longer muzzles than the males in five of seven populations in which muzzle length/frontal length values are available for at least four adults of each sex, the means for all populations measured are almost identical. In males they range from 0.648 to 0.715 (mean 0.686), in females from 0.667 to 0.707 (mean 0.669).

Caudodorsal scale row reduction occurs more posteriorly in males than in females. The reduction formulas for UF 12187-4, an adult male from Charleston County, South Carolina, and UF 12183, an adult female from Hyde County, North Carolina, are presented below.

UF 12187-4 ♂

$$17\frac{2(1)}{3(1)}\ 15\frac{2(2)}{2(3)}\ 13\frac{2(4)}{}\ 12\frac{4(2)}{3(5)}$$

$$10\frac{4(1)}{4(15)}\ 9\frac{3(1)}{3(4)}\ 6\frac{+3(1)}{3(63)}\ 5\frac{2(1)}{2(111)}\ 2(117)$$

UF 12183 ♀

$$12\frac{2(1)}{2(2)}\ 12\frac{2(2)}{2(3)}\ 10\frac{2(6)}{+4(7)}\ 9\frac{3(2)}{3(30)}$$

$$6\frac{3(29)}{3(97)}\ 4\frac{2(102)}{2(106)}\ 2(107)$$

Ontogenetic Variation

In certain populations the mean number of ventrals or subcaudals in juveniles is higher than that of adults, in some it is lower, and in still others it is identical.

There is apparently no consistency to this variation. Newly born T. sauritus have proportionally shorter tails than do the adults (Table 6). Coefficient of ontogenetic divergence values are comparable with those obtained for one population of T. proximus except in the case of southern Florida females which exhibit almost no change in proportional tail length from birth to adulthood (Table 6). Females of two broods from southern Florida (Broward and Collier Counties) are unique in having proportionally longer tails than the males of the same brood; the situation is reversed in the adults.

In the Great Lakes region and in northwestern peninsular Florida, where adults have either a black or very dark brown dorsum, the dorsum of juveniles is approximately the same shade of brown as in juveniles from areas where there is no pronounced darkening of the dorsum with age.

Individual Variation

Characters which neither vary geographically nor show sexual or ontogenetic variation are discussed below. Data on head scales refer to one side only. Individual variation in meristic characters is summarized in Table 12.

Oculars

None of the 957 T. sauritus examined has more than one preocular. Postoculars are usually 3, with 4 the most frequent variation.

Table 14.--Individual variation of meristic characters in Drosophila melanogaster

	Pre-orbitals	Post-orbitals	Anterior temporals	Posterior temporals	Supra-labials	Infra-labials		Inter-orbitals	Dorsal scale rows
Males	1(303)[a]	2,3 (2) 3 (339) 3,4(17) 3,5 4 (4)	1 (345) 1,2(14) 2 (21)	1 (3) 1,2 (7) 1,3 2 (301) 2,3 (33) 3 (11) 3,4 (2)	6,7 (2) 7 (228) 7,8(37) 8 (90) 9	7,8 8 (2) 8,9 (3) 8,10 9 (11)	9,10 (34) 9,11 (3) 10 (268) 10,11(14)	1 (21) 2(290) 3 (23) 4	17-19-17 (3) 19-17-17 (4) 19-18-17 19-19-16 (3) 19-19-17(327) 19-19-18 19-19-19 19-21-18
Females	1(594)	2 2,3(10) 3 (537) 3,4(34) 4 (13) 4,5	1 (681) 1,2(56) 2 (50)	1 (17) 1,2 (13) 1,3 (2) 2 (408) 2,3(105) 3 (47) 3,4	6 6,7 (3) 7 (347) 7,8(51) 8 (809) 8,9	8 (4) 8,9 (6) 8,10 (4) 9 (34) 9,10(50)	9,11 10 (464) 10,11(11) 10,12 11	0 (2) 1 (34) 2(436) 3 (68) 4 (4)	17-18-17 18-19-17 19-17-16 19-17-17 (19) 19-19-16 (3) 19-19-17(536) 19-19-18 19-19-19 21-19-17

[a] Single numbers indicate that both sides of the head have the same count; the number within the parentheses is the number of individuals when there is more than one.

Temporals

There is usually 1 anterior and 2 posterior temporals, but this character is highly variable. Unlike T. proximus, there is no population which has a high incidence of fragmentation of the anterior portion of the anterior temporal.

Supralabials

The number of supralabials varies geographically; the infrequent interposition of small scales between 4 of the normal supralabials does not vary in this manner.

Infralabials

Ten is the usual number, 9 the most frequent variation. Infralabial number is more variable in gaurinus than in proximus. Ten individuals of gaurinus have 2 more infralabials on one side of the head than on the other; no specimens of proximus have that large a difference between the 2 sides of the head.

Intermentals

Two is the usual condition; 3 is the most frequent variation, but it does not have a high incidence of occurrence in any population.

Ventrals

Anomalous scutes between the terminal ventral and the anal plate occur in 9.0 percent of the specimens examined; 4.5 percent, including a few of those just mentioned, have partial scutes elsewhere on the venter.

Subcaudals

Fusion of 1 or more pairs of subcaudals occurs in 2.2 percent of the material examined.

Dorsal scale rows

The great majority of individuals examined have the typical 19-19-17 formula; only two animals have a maximum number of rows in excess of 19.

Dorsal scale row reduction

Reduction takes place by loss of row 4 on both sides of the body in 36 of the 58 specimens examined for this character, and the fourth row is involved in the reduction on one side of the body in all but three of the remaining individuals. These three lose the fifth row on both sides. One snake drops row 6 on one side of the body.

The reduction occurs opposite ventrals 76 through 106 (mean 89.3) in males, 71 through 101 (mean 87.0) in females. There appears to be a rough, positive correlation between total number of ventrals and point of dorsal scale row reduction, but the correlation does not seem to be as strong as that observed in proximus.

Pattern and coloration

Presence or absence of parietal spots, and size when present, vary individually as does extent of the black post-orbital vitta and width of the black paravertebral stripes which border the vertebral stripe.

Geographic Variation

Although T. sauritus has a smaller range than T. proximus, it nevertheless exhibits a considerable amount of geographic variation, some of the patterns of character distribution being even more complex than those observed in proximus. As in the discussion of proximus, all meristic and proportional data presented below are based on population samples.

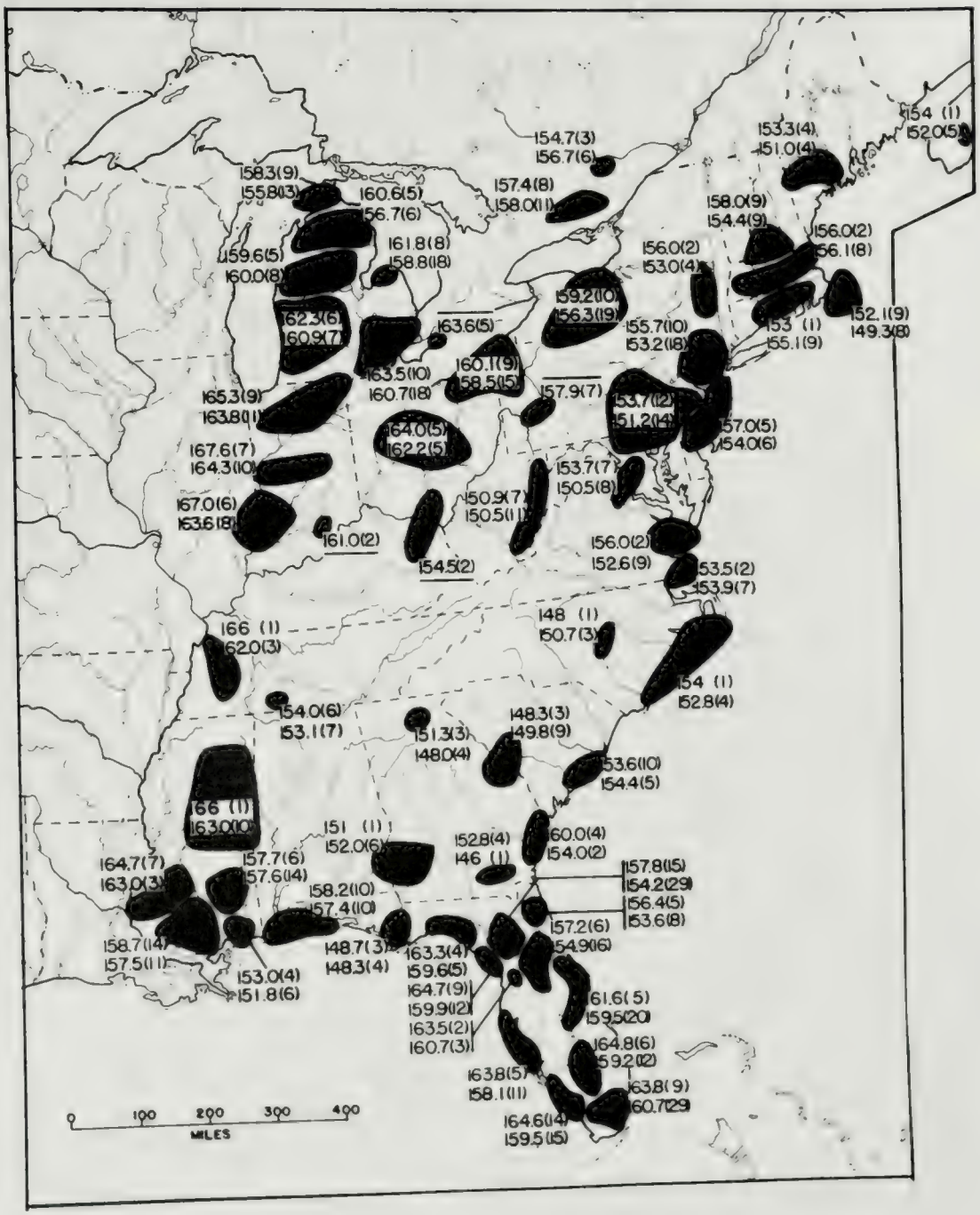
Supralabials

Throughout peninsular Florida to the vicinity of Tallahassee in the west, the Okefenokee Swamp region in the north, and through coastal Georgia north to Jasper County, South Carolina, 91.8 percent of the snakes have 8 supralabials on both sides of the head and 5.5 percent have 8 on one side. A rare variation, the presence of 9 supralabials, occurs only in eastern Florida. Throughout the rest of the range of this species, only 9.1 percent of the specimens have 8 on both sides. Another 10.8 percent have 8 on one side, 7 on the other. Almost all of the remaining 80.1 percent have 7 supralabials on both sides of the head. The few that do not, have 6 on one or both sides and all but one of these animals is from Michigan.

Ventrals

Variation in number of ventrals is exceedingly complex and can best be visualized by reference to figure 9. In southeastern Louisiana and adjacent Mississippi,

Figure 9.--Geographic variation in ventral number of [illegible] in the United States and Canada. Black blotches represent the areas from which samples were taken. The upper numbers associated with each blotch are the sample mean and sample size (in parentheses) for males; the lower numbers present the same data for females. When a line appears in place of either the upper or lower numbers, it signifies that no specimens of that sex were present in the sample.


154 (1)
152.0(5)
153.3(4)
151.0(4)
154.7(3)
156.7(6)
158.3(9)
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156.7(6)
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154.4(9)
156.0(2)
156.1(8)
159.6(5)
160.0(8)
161.8(8)
158.8(18)
156.0(2)
153.0(4)
159.2(10)
156.3(19)
162.3(6)
160.9(7)
163.6(5)
155.7(10)
153.2(18)
153 (1)
155.1(9)
152.1(9)
149.3(8)
163.5(10)
160.7(18)
160.1(9)
158.5(5)
157.9(7)
165.3(9)
163.8(1)
153.7(12)
151.2(14)
157.0(5)
154.0(6)
164.0(5)
162.2(5)
167.6(7)
164.3(10)
153.7(7)
150.5(8)
167.0(6)
163.6(8)
150.9(7)
150.5(11)
161.0(2)
154.5(2)
156.0(2)
152.6(9)
153.5(2)
153.9(7)
148 (1)
150.7(3)
166 (1)
162.0(3)
154 (1)
152.8(4)
154.0(6)
153.1(7)
148.3(3)
149.8(9)
151.3(3)
148.0(4)
153.6(10)
154.4(5)
166 (1)
163.0(10)
151 (1)
152.0(6)
152.8(4)
146 (1)
160.0(4)
154.0(2)
164.7(7)
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157.7(6)
157.6(14)
157.8(15)
154.2(29)
156.4(5)
153.6(8)
158.2(10)
157.4(10)
157.2(6)
154.9(16)
158.7(14)
157.5(11)
153.0(4)
151.8(6)
148.7(3)
148.3(4)
163.3(4)
159.6(5)
164.7(9)
159.9(12)
163.5(2)
160.7(3)
161.6(5)
159.5(20)
164.8(6)
159.2(12)
163.8(5)
158.1(11)
163.8(9)
160.7(29)
164.6(14)
159.5(15)
0
100
200
300
400
MILES

males have a mean of 158.7 ventrals, females 157.5. Population samples from southeastern Mississippi (exclusive of the Biloxi area) and the Mobile Bay--Pensacola Bay area agree closely, but the snakes in southwestern Mississippi have a mean of 6 to 7 more ventrals in males, 5½ in females. From thence north-northeastward to northern Indiana (exclusive of central Tennessee) the mean number of ventrals in females is almost invariable. The mean for males increases slightly over this distance and reaches its peak (157.6) in central Indiana. In northern Indiana males the mean is about 2½ scales less and it decreases gradually but steadily northward in Michigan to the Straits of Mackinac, the mean in extreme northern Michigan being reduced by another 3 scutes. The female mean ventral count drops by 3 scales between northern Indiana and southern Michigan, then reduces more gradually northward, being another 5 scales less in extreme northern Michigan. A series of females (no males available) from extreme southern Ontario agrees well with females of northern Indiana, and those from central Ohio have only slightly lower means. Northeastward from these populations the mean number of ventrals in both sexes decreases abruptly, by about 4 scales in populations south of Lake Erie, and then tapers off gradually in western New York and eastern Ontario. A series of seven females (no males available) from the vicinity of Pittsburgh agrees closely with females

from the northeastern Ohio--northwestern Pennsylvania area in mean ventral number. One hundred miles to the south, in eastern West Virginia, the mean number of ventrals in both sexes decreases abruptly; there are 7½ scales less in females. There also appears to be a clinal reduction in ventral number from central Ohio into West Virginia and eastern Kentucky. The reduction in this case is also abrupt, a decrease of 11½ (females) to 13 (males) taking place over a distance of less than 200 miles.

The snakes in central Tennessee have means at least 9 scales less than those of the populations to the west of the Tennessee River. A series from the vicinity of Biloxi, Mississippi, has a mean of 5 to 6 fewer ventrals than the populations surrounding it and no more than 90 miles distant. Snakes from southeastern Alabama and southern Georgia (exclusive of the coast) appear to be similar to the Biloxi animals in mean ventral count, but more specimens are needed to determine just how well they agree, and if the two are connected by populations in southwestern Alabama north of Mobile Bay.

One hundred-and-fifty miles east of the Mobile Bay--Pensacola Bay area in the Apalachicola River valley the mean number of ventrals decreases by more than 9 scales. The populations just to the north in southern Georgia have means less than 4 scales higher. A single adult female (UF 7365) from St. Vincent's Island off the mouth of the

Apalachicola River has 161 ventrals, almost 13 more than the mean for the Apalachicola Valley series. From thence eastward and southward in the western coastal lowlands to southern Florida, and northward in the eastern coastal lowlands to about the latitude of Daytona Beach, the mean number of ventrals is remarkably constant, ranging from 163.3 to 164.8 in males, 159.4 to 160.7 in females (females of the west-central Florida and males of the east-central Florida populations have means 1 to 2 scales less than those just mentioned). In the central highlands of Florida and in the eastern coastal lowlands north of Daytona Beach, ventral counts abruptly decrease, the means ranging from 156.4 to 157.8 in males, 153.6 to 154.9 in females. Ventral number falls off sharply to the north in inland Georgia, but on the coast it varies from the mean range stated for northern Florida by less than 1 scute in females and less than 3 in males (larger series of males will undoubtedly reduce the variance in means) from northeastern Florida to central New Jersey, thence inland up the west side of the Hudson River to the vicinity of Albany, New York. On or adjacent to the Piedmont from the Savannah River to southeastern Pennsylvania, mean ventral counts are 2 to 4 scales less than on the outer Atlantic Coastal Plain. In these inland populations the number of mean ventrals increases to the north, but by less than 1½ scales in females, somewhat more in males (too few males are

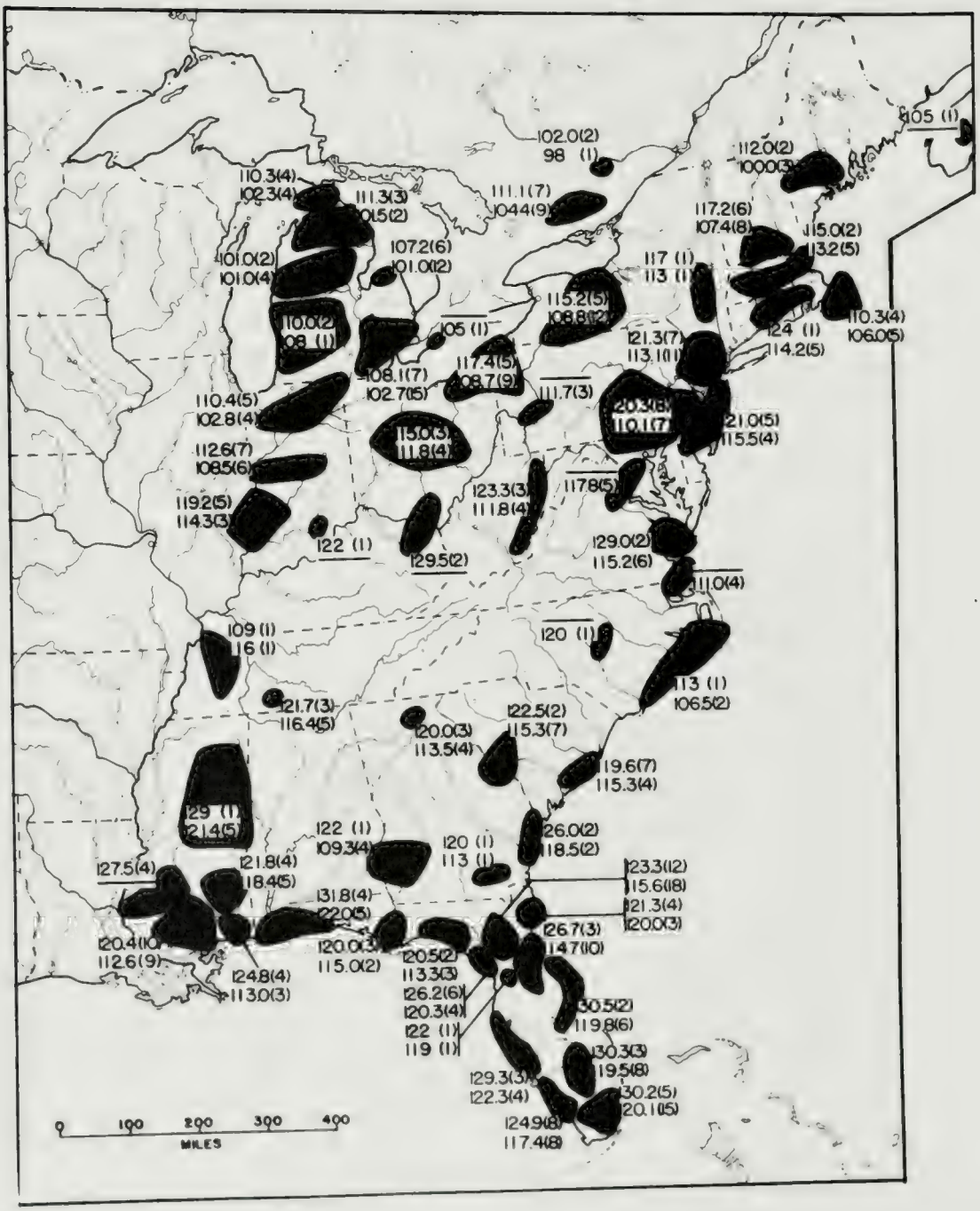
available from the southern localities). These populations agree rather well in mean number of ventrals with those located in extreme northern Georgia and eastern West Virginia.

On Long Island and at scattered localities in New York east of the Hudson River as far north as Lake George, the ventral count in females rises abruptly to a mean of 158.0; there is virtually no change in males. As counts in New England females are somewhat lower, this change does not appear to be associated with any clinal trends. In central New England means for females range from 154.4 to 156.1; only the southern New Hampshire sample has a sufficient number of males to place any reliance on the resulting mean (i.e., 158.0). Thus, these populations show a slight increase in ventral number over the relatively stable Atlantic Coastal Plain series, but this trend is abruptly reversed in southeastern Massachusetts, Maine, and Nova Scotia, where the means are between 154.1 and 154.0 in males, 149.3 and 154.0 in females.

Subcaudals

Variation in subcaudal number appears to be almost chaotic when viewed in terms of local populations, and a meaningful evaluation is further hampered by having so few individuals with a complete tail in the majority of the series examined. A generalized pattern can be described, but see Figure 10 for details. Mean subcaudal counts in

Figure 10.—Geographic variation in subcaudal number of Lampropeltis getulus in the United States and Canada. Black blotches represent the seven taxa which samples were taken. The upper numbers associated with each blotch are the sample mean and sample size (in parentheses) for males; the lower numbers present the same data for females. When a line appears in place of either the upper or lower numbers, it signifies that no specimens of that sex were present in the sample.


102.0(2)
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112.0(2)
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110.3(4)
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101.5(2)
111.1(7)
104.4(9)
117.2(6)
107.4(8)
115.0(2)
113.2(5)
101.0(2)
101.0(4)
107.2(6)
101.0(2)
117 (1)
113 (1)
115.2(5)
108.8(12)
110.0(2)
108 (1)
105 (1)
124 (1)
114.2(5)
110.3(4)
106.0(5)
121.3(7)
113.1(1)
117.4(5)
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108.1(7)
102.7(5)
111.7(3)
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110.1(7)
121.0(5)
115.5(4)
115.0(3)
111.8(4)
112.6(7)
108.5(6)
123.3(3)
111.8(4)
117.8(5)
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114.3(3)
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129.5(2)
129.0(2)
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111.0(4)
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124.9(8)
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0 100 200 300 400
MILES

in males almost always exceed 120 in the area south of the Ohio River on the west, and as far north as southeastern Pennsylvania, northern New Jersey, and possibly Connecticut on the east. Within this area the means exceed 125 in eastern Virginia, coastal Georgia, the southern four-fifths of peninsular Florida, the Mobile Bay--Pensacola Bay area (the highest mean, 131.8, occurs here), southwestern Mississippi, and northern Mississippi. The mean number decreases to the north, males from populations in northern Indiana, Michigan, Ontario, and Maine not having over 112. Females from this northern area have less than 105 mean ventrals. The mean number in females increases southward, rarely being less than 112 south of New Hampshire, southeastern New York, Pennsylvania, Ohio, and central Indiana. The mean exceeds 120 in females from northeastern Florida, southeastern Florida, west-central Florida (the highest mean, 124.3, occurs here), Levy County, Florida, the Mobile Bay--Pensacola Bay area, and northern Mississippi.

Proportions

Relative tail length is fairly constant in the area lying south of the Ohio River, and in southern Pennsylvania, New Jersey, and southeastern New York. Means of tail length/total length values in males usually fall between 0.345 and 0.355, in females between 0.335 and 0.345. Means are in excess of 0.360 in males from central Tennessee and the mid-Savannah River area, and as high as

0.378 in a small series from eastern West Virginia. In three New England series the mean for males is 0.343 as compared to 0.352 in New Jersey, in females it has decreased from 0.342 to 0.330. The one male available from Nova Scotia (AMNH unnumbered) has a value of 0.310. Males from western New York, northwestern Pennsylvania, Ohio, and southern Indiana have means ranging from 0.347 to 0.336; means in females range from 0.317 to 0.319. In northern Indiana and Michigan means in males range from 0.310 to 0.315, in females from 0.299 to 0.308. In eastern Ontario the mean for females is 0.312.

Pattern

The vertebral stripe is frequently poorly developed or lacking in the snakes inhabiting peninsular Florida and southeastern Georgia. Since the stripe in this area is tan in color, often only a shade lighter than the color of the dorsum, the loss of the stripe is brought about merely by elimination of the narrow, black borders of the vertebral stripe. There is almost always at least a faint indication of a stripe for a short distance immediately in back of the head. Throughout the rest of the range the vertebral stripe is always present and distinctly margined by the black paravertebral stripes although the latter may vary greatly in width. In the Great Lakes region, where the dorsum is usually black or nearly black, the stripe is often narrower and involves somewhat less than one-half the

width of each paravertebral row of scales (in addition, of course, to all of the vertebral row). The vertebral stripe in *V. ureinus* is also frequently narrower in the northern part of the range.

In peninsular Florida and southeastern Georgia the lateral stripe is narrow, always occupying less than half of one of the two rows on which it is situated, and usually less than half of both rows. In the region of the Great Lakes, dorsal scale row 2 is frequently involved in the lateral stripe to a slight degree on the anterior portion of the body in addition to the normal 3 and 4, thus paralleling the condition typical of *Thamnophis butleri*, a species which inhabits part of this same area. The condition cannot be said to typify members of the populations in this region, but it does have a much higher frequency of occurrence here than elsewhere in the range of the species. Animals with an anteriorly widened lateral stripe have also been observed in samples from central Tennessee, eastern West Virginia, and western Pennsylvania, where they are not associated with a black dorsum. CAS 15680 from West Virginia and MMC 3090-2 from Nova Scotia have rows 3, 4, and 5 incorporated in the lateral stripe.

Coloration

The dorsum is tan or brown in peninsular Florida and coastal Georgia, except in western Levy County, Florida, and thence northwestward along the coast to a point almost

due south of Tallahassee. In this area the dorsum is usually a very dark brown to black in color. It is also black or very dark brown in Nova Scotia, Maine, and the Great Lakes region. Southward throughout the rest of the range (except peninsular Florida and coastal Georgia) the dorsum is a reddish brown.

In ribbonsnakes from peninsular Florida and southeastern Georgia the vertebral stripe is usually some shade of tan, occasionally with a metallic luster, or is lacking. Outside this area it is usually some shade of yellow, occasionally overlain with dark pigment in the Great Lakes region.

The lateral stripe is yellow throughout most of the range of the species; it is occasionally white at scattered localities on the Florida peninsula. In western Levy County and in the coastal area to the northwest, the lateral stripe is usually a light blue or bluish white.

Discussion

Geographic variation is for the most part of the discordant type discussed previously in conjunction with *T. proximus*. Like that species, *T. sauritus* has two major zones of concordant character transition. There is an abrupt change in supralabial number, lateral stripe width, vertebral stripe color, and also a slight change in color of the dorsum between the peninsular Florida--southeastern Georgia area and the region to the north and west. This

transition may be related to the fact that most of peninsular Florida is believed to have been isolated from the mainland, in the form of islands, during shifts in the level of Pleistocene seas.

The other transition zone appears to be associated to a certain degree with the southern limits of Pleistocene glaciation, the animals occupying the previously glaciated area having a darker dorsum, a relatively shorter tail, and fewer subcaudals than are found in the populations south of the glacial boundary. This relationship breaks down in northern New Jersey, eastern New York, and southern New England where long-tailed snakes with a brown dorsum and high subcaudal counts range well into glaciated territory.

The elements of color pattern have less observable geographic variability in *V. saurutus* than does the number of ventrals or subcaudals.

Taxonomy

The population samples examined appear to represent four major populations which replace each other geographically. These are defined on the basis of differences chiefly in color pattern, but also to some degree in scutellation and proportions. The salient features of these populations are discussed below within the framework of their formal description as subspecies.

The following key for distinguishing adults of the four races of T. sauritus was designed primarily for use with live material. If only preserved specimens are available, attention should be paid to geographic provenance of the sample.

Key to the Subspecies of Thamnophis sauritus

1. Supralabials 7, occasionally 8; vertebral stripe some shade of yellow; lateral stripe not narrow, occupying 1/2 or more of both rows 3 and 4 2

1'. Supralabials 6, rarely 7; vertebral stripe tan, or lacking, lateral stripe narrow, occupying less than 1/2 of either row 3 or 4, or both 3

2(1). Dorsum reddish brown; lateral stripe rarely widened anteriorly; tail relatively long (mean tail length/total length usually exceeding 0.340 in males, 0.330 in females) . . . . . T. s. sauritus (p. 119)

2'(1). Dorsum velvety black or very dark brown; lateral stripe frequently widened anteriorly, involving row 4; tail relatively short (mean tail length/total length usually not exceeding 0.335 in males, 0.340 in females) . . . . . T. s. septentrionalis (p. 121)

3(1'). Dorsum tan or brown, rarely very dark; lateral stripe yellow, occasionally white . . . . . T. s. sackeni (p. 126)

3'(1'). Dorsum very dark brown or black; lateral stripe bluish white or light blue, occasionally white . . . . . T. s. sirtalis (p. 130)

Accounts of Subspecies

Thamnophis sauritus sauritus (Linnaeus)

Thamnophis sauritus sauritus Anthony, Lydd: 114 [by implication]

Neotype. The data presented for the species (p. 92) apply here.

Definition. A subspecies of Thamnophis sauritus characterized by 7 supralabials, a reddish brown dorsum, a golden yellow vertebral stripe, and a relatively long tail.

Range. The nominate race ranges from southern New England, eastern New York, New Jersey, and eastern Pennsylvania, westward through southern Ohio and southern Indiana to the Mississippi River, south to the northern edge of Lake Pontchartrain on the west and to northwestern Florida and Georgia (exclusive of the southeastern third of the state) on the east.

Description of neotype. Scutellation is as follows:[1] oculars 1+3, temporals 1+3, supralabials 7, infralabials

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[1]Data on scutellation and proportions are from Schmidt and Conant (1956-57).

10, dorsal scale rows 19-19-17, ventrals 156, subcaudals 113. Body length is 388 mm., tail length 40+ mm., tail length/total length ratio 0.34[0.342 if carried to another decimal place].

Inasmuch as Schmidt and Conant's (1936-37) description of the neotype is based on a preserved specimen, the following color notes are presented for UF 14187-1, an adult male collected 1.5 miles n Mayesol, Charleston County, South Carolina, by Rita J. Rossman and Douglas A. Rossman: dorsum reddish brown (Ridgw. and Paul 14k12), a shade lighter below the lateral stripe; vertebral stripe golden yellow (12d2); lateral stripe light yellow (13l1); venter cream (9f1); dark ventrolateral stripe broad, occupying 1/4 the width of a ventral scute on each side; chin shields and infralabials white, supralabials yellowish white. The light postocular spot is confined to the lower postocular; the black postorbital vitta is broad. The tiny parietal spots are separate and yellow, margined narrowly with black.

Discussion. Meristic and proportional characteristics of the nominate race may be summarized as follows: 2 to 4 postoculars; 1+1 to 2+3 temporals; 6 to 8 supralabials; 8 to 11 infralabials; 1 to 4 intergenials; 17-18-17 to 19-19-17 dorsal scale rows; males 149-166, females 142-169 ventrals; males 106-130, females 90-130 subcaudals. Males range from 144.5 to 451 mm. in body length, 185 to

665 mm. in total length; adult tail length/total length ratio 0.333 to 0.388. Females range from 149 to 636 mm. in body length, 190 to 956 mm. in total length; adult tail length/total length ratio 0.317 to 0.388.

My concept of the color pattern in T. s. sauritus is based on living specimens from Cape May, Sussex, and Warren Counties, New Jersey; Hyde County, North Carolina; Charleston County, South Carolina; Barbour County, Alabama; and Forrest County, Mississippi, as well as a colored slide of a snake from Burlington County, New Jersey, and color notes on one from Tolland County, Connecticut (the slide and color notes were contributed by Robert K. Grant, Jr., and Dan Sweet, respectively). Intergradation between T. s. sauritus and T. s. nitalis, and between sauritus and septentrionalis, is discussed later.

Thamnophis sauritus septentrionalis,[1] new subspecies

Holotype. UF 12179-2, an adult female from Michigan Hollow, near Ithaca, Tompkins County, New York, collected 20 May 1959 by John A. Bartley.

Definition. A subspecies of Thamnophis sauritus characterized by 7 supralabials, a velvety black or very dark brown dorsum, a yellow vertebral stripe, often overlain with brown pigment, and a relatively short tail.

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[1]refers to the northern distribution of this race in relation to the range of the species.

Range. This subspecies extends from Nova Scotia, Maine, and possibly central New Hampshire west through southern Ontario and western New York to extreme northern Michigan and central Indiana. There may be an isolated colony in northeastern Wisconsin (see Discussion).

Description of holotype. Scutellation is as follows: oculars 1+3, temporals 1+2, supralabials 7, infralabials 10, intergenials 4, dorsal scale rows 19-19-17, ventrals 150, subcaudals 108. Body length is 574 mm., tail length 471 mm., tail length/total length ratio 0.341.

The dorsum is velvety black on the anterior 2/3 of the body, very dark brown posteriorly; below the lateral stripe the dorsum is dark brown (Ridgway and Paul 7215). The vertebral stripe is yellow, but so heavily overlain with brown that it is impossible to determine the exact shade; the lateral stripe is a light yellow (16D1). The venter is pale green suffused throughout with tan; the dark ventrolateral stripe is broad, occupying 1/5 the width of a ventral on each side. The chin shields and inframalabials are white, the supralabials a pale greenish white. The head is black, hence no postorbital vitta is visible; the parietal spots are lacking.

Discussion. Meristic and proportional characteristics of this subspecies are as follows: 4 to 5 postoculars; 1+1 to 2+3 temporals; 6 to 8 supralabials; 7 to 11 infralabials; 1 to 3 intergenials; 16-17-17 to 19-21-19

dorsal scale rows; males 152-177, females 148-159 ventrals; males 98-143, females 94-114 subcaudals. Males range from 125.5 to 433 mm. in body length, 179 to 654 mm. in total length; adult tail length/total length ratio 0.298 to 0.333. Females range from 128 to 574 mm. in body length, 164 to 845 mm. in total length; tail length/total length ratio 0.288 to 0.335.

In defining T. s. sackenii and in attempting to delimit its range, I have had access to living ribbon-snakes from Monroe and Tompkins Counties, New York; Trumbull County, Ohio; Hillsdale and Washtenaw Counties, Michigan; and Marshall County, Indiana, as well as colored slides of two live individuals from Honey Harbour, Ontario, and color notes on a series of specimens from Rondeau Provincial Park, Ontario (the slides and notes were generously provided by Bruce Kingsbury). Each of these animals has a dorsum which is black or very dark brown on at least the anterior half of the body, usually more.

Locating the zone of intergradation between proximus and sackenii by examination of preserved specimens is made difficult by the fact that what was a black dorsum in life may become a dark brown dorsum after several years storage in preservative, particularly if the animal was approaching ecdysis at the time of its preservation. Nevertheless, by cautiously treating color garnered from preserved specimens and by utilizing relative tail

length values and the color data available from live material, some estimate of the southern range limits of this subspecies may be made. A much more accurate delimitation will be possible when more live specimens or color notes become available.

The northern Indiana population clearly belongs to septentrionalis, the central Indiana snakes appear to be close to that subspecies (although they may possibly be intergrades), and the series from southwestern Indiana--southeastern Illinois either represents sauritus x septentrionalis intergrades or sauritus. Two adult males (UMMZ 107910, 108092) from the Muscatatuck River in southeastern Indiana near the glacial boundary appear to be sauritus. The zone of intergradation probably extends through central Ohio. The color pattern of a live adult female from Licking County in south-central Ohio is typical of sauritus, but the snake also has a relatively short tail. UMMZ 756 from Jackson County in the southern part of the state is definitely a sauritus. Northeastern Ohio ribbonsnakes are members of the northern race, and so presumably are the populations in adjacent Pennsylvania although their status is not clearly understood. Ribbonsnakes from the vicinity of Pittsburgh probably are intergrades. All the West Virginia animals examined appear to be sauritus, with the possible exception of UMMZ 45147 from Preston County which appears to have a black dorsum,

although all other characters agree with the nominate form.

The eastern New York and southern and central New England ribbonsnakes all appear to be sauritus, but the southern New Hampshire sample may be representatives of an intergrade population. I have included the small series from Maine as septentrionalis because it appears that these animals may have had a black dorsum in life, and at least one of them (MCZ 699) shows anterior widening of the lateral stripe. This population seems to be disjunct from the main body of the range of septentrionalis, but the literature records for Essex and Franklin Counties, New York (Weber, 1928, and Evermann, 1918, respectively), probably are based on members of this race, and future collecting in central New Hampshire and central Vermont may well close the gap. Bleakney (1951) notes that the T. sauritus he collected in Nova Scotia were black, with yellow stripes. The only specimen of that series which has a complete tail (KUMZ unnumbered) has the low tail length/total length value characteristic of T. s. septentrionalis. This population is unquestionably a relict; the probable cause of the disjunction is discussed by Bleakney (1958).

Dickinson (1950) reports that H. A. Suzuki observed a ribbonsnake at Bass Lake, Marinette County, Wisconsin, but that the specimen was not preserved. Nevertheless, there is a specimen of T. sauritus in the Milwaukee Public Museum collection (MPM 1649) which is listed as having been

collected by Suzuki in Marinette County at Bass Lake. Despite this confusion, the specimen agrees fairly well with Michigan subterriqualis in details of constellation, and row 4 is clearly involved in the lateral stripe on the anterior part of the body. Hence it is altogether possible that an isolated colony of subterriqualis does exist in northeastern Wisconsin and the upper peninsula of Michigan.

Thamnophis sauritus sackeni (Kennicott)

Eutaenia sauritus var. sackenii Dumeril and Bocourt, 1870: 759

Thamnophis sauritus sackeni Ruthven, 1908: 107

Thamnophis sauritus sackenii Blanchard, 1925: 18

Holotype. The holotype, which was collected in Florida by Baron Osten Sacken, is apparently lost. Dr. Doris M. Cochran has informed me that USNM 4501 (now lost) is listed in the U.S. National Museum catalogue as a type of Eutaenia sackenii. This specimen probably should be considered a paratype inasmuch as the original description was based on one or more specimens in the collection of Northwestern University. Kennicott's only reference to the existence of additional material in the U.S. National Museum was contained in a footnote, and it is not certain whether he considered this material to be a part of the type series. A neotype has not been designated because the original description (Kennicott, 1859) and the type locality adequately serve to associate the name to a

specific population. Schmidt (1953) restricts the type locality to Gainesville, Alachua County, Florida, and I see no reason to dispute this restriction.

Definition. A subspecies of Thamnophis sauritus characterized by 8 supralabials, a tan to brown dorsum, a tan vertebral stripe, often with a metallic luster, a narrow lateral stripe, and a relatively long tail.

Range. This race is distributed throughout peninsular Florida (exclusive of western Levy County and the coastal area to the northwest of it) west to the vicinity of Tallahassee, and north through the Okefenokee Swamp and coastal Georgia to Jasper County, South Carolina. Apparently there is an isolated colony on St. Vincent's Island just west of the mouth of the Apalachicola River.

Description. Inasmuch as the holotype is lost, the following description is based on UF 12145-2, an adult female from 4.5 miles E Ross Bluff, Marion County, Florida, collected by Alfred T. Neill and Sam A. Telford, Jr. Scutellation is as follows: oculars 1+3, temporals 1+2, supralabials 8, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 151, subcaudals 114. Body length is 458 mm., tail length 223 mm., tail length/total length ratio 0.347.

The dorsum is brown. The vertebral stripe is metallic tan, the lateral stripe pale yellow and narrow, the stripe occupying slightly less than 1/2 the width of a scale on rows 3 and 4. The venter is pale greenish yellow,

pale green on the tail; the dark ventrolateral stripe is broad, occupying slightly more than 1/4 the width of a ventral scute on each side. The chin shields and lower part of the infralabials are white, the supralabials and upper part of the infralabials pale yellow. The parietal spots are lacking.

Discussion. Meristic and proportional characteristics of this subspecies may be summarized as follows: 2 to 5 postoculars; 1+2 to 2+3 temporals; 7 to 9 supralabials; 8 to 12 infralabials; 0 to 3 intergenials; 19-17-17 to 19-19-17 dorsal scale rows; males 150-171½, females 146-166 ventrals; males 116-134, females 105-131 subcaudals. Males range from 144 to 537 mm. in body length, 415 to 803 mm. in total length; adult tail length/total length ratio 0.343 to 0.384. Females range from 137 to 670 mm. in body length, 407 to 1013 mm. in total length; adult tail length/total length ratio 0.317 to 0.364.

I have seen living examples of this subspecies from Alachua, Brevard, Broward, Collier, Dade, Duval, Hendry, Lake, Levy, Manatee, Marion, Martin, and Palm Beach Counties, Florida, and a colored slide of one from Charlton County, Georgia, provided by Barry and Norma Hottman. I have also examined a living specimen (no longer available) from near Ridgeland, Jasper County, South Carolina, which is either a *pachyura* or a *pachyura* × *pachyuri* intergrade. The vertebral and lateral stripes of this animal are not brightly colored, and the dorsum is more of

a tan than a reddish brown, all of these items being more characteristic of sackeni. On the other hand, the snake has 7 supralabials on both sides of the head, a condition found in sackeni only on the periphery of the range where genetic influence from sauritus would be expected. Furthermore, the color of the vertebral stripe is not characteristic of that usually found in either form, and the lateral stripe is not especially narrow. Another Jasper County specimen (UF 12136, from the Savannah National Wildlife Refuge) has the narrow lateral stripe typical of sackeni, and the vertebral stripe also appears closer to the type found in that race. The dorsum, after storage in alcohol for a year, appears to be a light reddish brown. Specimens from coastal Georgia, despite a high incidence of 7 supralabials, appear to be fairly typical of sackeni. Thus, sackeni apparently extends along the coast as far north as the Savannah River, intergrading with sauritus in extreme southern South Carolina.

Inland, a series from the Okefenokee Swamp is, I believe, unquestionably sackeni in spite of frequent occurrence of 7 supralabials. Neill (1954) expresses the opinion that animals from as far inland as Emanuel County, Georgia, and Barnwell County, South Carolina, are closer to sackeni than to sauritus, and that sauritus does not occur below the Fall Line in eastern Georgia; I have not seen specimens from Emanuel County, but I find the sample from

just below the Fall Line in eastern Georgia and adjacent South Carolina to be fairly typical of sauritus.

Two adult females (UMMZ 106434-435) from Lake Miccosukee, Jefferson County, Florida, are sackeni, although one of them has 7 supralabials on both sides of the head. They represent the westernmost locality at which this race has been taken, except for UF 7369, an adult female from St. Vincent's Island in Franklin County, Florida. This specimen definitely appears to be a sackeni, but all the specimens which have been collected on the adjacent mainland are good examples of sauritus. Only further collecting can resolve this problem. All specimens available from southwestern Georgia appear to be sauritus. Intergrades between sackeni and nitae will be discussed under the latter race.

Thamnophis sauritus nitae,[1] new subspecies

Holotype. UF 12150-2, an adult female from McDonald Slough, St. Marks National Wildlife Refuge, Wakulla County, Florida, collected on 16 May 1959 by Nita J. Rossman and Douglas A. Rossman.

Definition. A subspecies of Thamnophis sauritus characterized by 8 supralabials, a very dark brown or black dorsum, on at least the anterior part of the body,

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[1] Named in honor of my wife Nita, who collected our first living example of this strikingly beautiful race, in appreciation of her clerical and field assistance.

with the vertebral stripe obscured or absent, a bluish white or light blue lateral stripe, and a relatively long tail.

Range. This subspecies occurs in the coastal lowlands of northwestern peninsular Florida from the Withlacoochee River on the south to the Wacissa River on the west.

Description of holotype. Scutellation is as follows: oculars 1+3, temporals 1+2, supralabials 8, infralabials 10, intergenials 3, dorsal scale rows 19-19-17, ventrals 160, subcaudal series and tail incomplete. Body length is 621 mm.

The dorsum is black for a short distance in back of the head, becoming a dark brown posteriorly (Maerz and Paul 15L12 at midbody) with much black pigment overlying the brown. The vertebral stripe is lacking; the narrow lateral stripe is light blue (34G1). The venter is bluish white anteriorly, becoming pale tannish yellow thereafter (the posterior margin of each scute is light bluish green); the dark ventrolateral stripe is broad, occupying 1/3 the width of a ventral on each side. The chin shields are white, the supralabials light blue at least posteriorly. The head is black, hence no postorbital vitta is visible; the parietal spots are lacking.

Discussion. Meristic and proportional characteristics of this subspecies are as follows: 3 to 4

postoculars; 1+2 to 2+2 temporals; 7 to 8 supralabials; 9 to 11 infralabials; 1 to 3 intergenials; 17-19-17 to 19-19-17 dorsal scale rows; males 161-169, females 156-166 ventrals; males 119-131, females 105-130 subcaudals. Males range from 190 to 534 mm. in body length, 440 to 756 mm. in total length; adult tail length/total length ratio 0.335 to 0.356. Females range from 146.5 to 621 mm. in body length, 410 to 701 mm. in total length; adult tail length/total length ratio 0.331 to 0.372.

I have examined living specimens of this race from Jefferson, Levy, Taylor, and Sabulia Counties, and a freshly killed specimen from Dixie County, all in Florida. All specimens from localities northwest of the Suwannee river are typical of this subspecies as defined above; the situation in Levy County is somewhat confusing. To the northwest of this county, miticeps occurs on the coast, with mackenii inland to the north and east. However, specimens collected in inland Levy County at or near Vista, Otter Creek, Gulf Hammock, and Inglis, all have the very dark brown dorsum and bluish white lateral stripe characteristic of miticeps. UF 12149 from 5 miles NW Lebanon Station has a black to very dark brown dorsum and a bright white lateral stripe. Those from western Levy County between Sumner and Wekiva appear to be a mixed population. UF 12139 and 12143, adult males from 1 mile NW Sumner are both fairly typical miticeps; UF 12133 and 12138, adult females from 3 miles

NW Sumner, and in UF 12140, an adult female from Lukens, the dorsum is dark brown for a few inches behind the head and brown thereafter. The vertebral stripe is clearly defined in all three. The lateral stripe in the Lukens specimen is bluish white, at least anteriorly; in the other two it is a dusky white.

These three animals could probably be dismissed as merely being variants of the more typical condition except for Neill's (1958) report that Cedar Key ribbonsnakes are fairly typical of sackeni (Neill was familiar with the dark, blue-striped form at that time, in fact reports collecting it near the mouth of the Steinhatchee River, Dixie County, in that same paper), and the existence of UF 12141, a subadult male from 4 miles NW Sumner, which resembles sackeni in all features save scutellation. The dorsum is dark brown, the vertebral stripe dark tan and distinct throughout the length of the body, and the lateral stripe very definitely a light yellow. These animals would undoubtedly be called intergrades if there were sackeni on the coast with which nitae could intergrade, but such a sackeni population appears to be lacking at the present time. Neill (1957) has demonstrated that there has been a relatively rapid subsidence of the Gulf Coast in post-Pleistocene times, and it seems possible that typical sackeni did at one time exist to the west of nitae. When the territory which it occupied sank beneath the surface of

the Gulf of Mexico, only the intergrade population remained to indicate that a coastal population of sackeni ever existed.

UF 14130, an adult female from 1 mile N Jamestown, has a brown dorsum and dusky white lateral stripe, and also appears to be a sackeni x nitae intergrade. This seems reasonable inasmuch as sackeni does occur on the coast to the south. Specimens from the vicinity of Lake Rosa Apopka in Orange County are considered to be sackeni x nitae intergrades, as is an adult female (UF 14142) from 4.5 miles SW Bronson, Levy County (this specimen would be referable to sackeni except for the color of the lateral stripe).

An adult female, UF 14413, poses another kind of problem. If the colors of the animal in life were at all close to those present in the preserved specimen, it would possibly qualify as a sackeni x nitae intergrade. The collecting data, however, indicate that the snake was taken 40 miles N Tallahassee in Calhoun County, Florida. The mileage given would place the locality at Telogia Creek, which is in Liberty County, rather than Calhoun. If these data are accurate, then sackeni, or a derivative, penetrates the range of typical sauritus (which occurs 3 miles NW Bosford, a locality less than 5 miles to the east) without giving any indication of intergradation. The specimen in question has 3 supralabials, 101 ventrals, and a tan vertebral stripe; the Bosford specimen (UF 7998, a

male) has 7 supralabials, 148 ventrals, and agrees equally well with typical sauritus in all other respects. I believe the locality data to be in error.

Within the range of Thamnophis sauritus nitae, another species of gartersnake, T. sirtalis, also has a very dark dorsum and a blue or bluish white lateral stripe. This situation will be detailed at a later date.

Evolutionary Trends

The distinctive features of each of the four geographic races of Thamnophis sauritus may reflect historical factors as much as adaptations to different environmental situations. Nevertheless, the black dorsum of sackenii, the frequent narrowing of its vertebral stripe, and the frequent overlaying of that stripe with brown pigment seem to indicate adaptations for absorption of solar radiation paralleling those found in the northern race of T. sirtalis. The brown young are almost identical with the young of T. s. sauritus, and it seems almost certain that sackenii represents a northern, more cold-tolerant, derivative of the nominate race.

The nominate subspecies is wide-ranging and apparently thrives under a great many environmental conditions. It may have evolved on the mainland at a time when the ancestral stock of the species (of which sackenii probably is the nearest present-day representative) was isolated on one or more of the islands that constituted Florida in

Pleistocene times. I am unable to suggest an explanation as to the adaptive significance, if any, of the very dark dorsum and blue lateral stripe present in the race <u>nitae</u>. It is entirely possible that there is none, and that the factor which is being selected is somehow associated with enzymes involved in the production of pigment. To human eyes, at least, this snake is much more conspicuous in each of the several habitats it occupies than would be the comparatively drab <u>sac.oni</u>.

<u>Natural History</u>

A brief summary of our knowledge of the ecology of <u>T. sauritus</u> is presented below. For a detailed account of this species in one part of its range (Michigan) see Carpenter (1952a, 1952b, and 1953).

Habitat

The eastern ribbonsnake utilizes a great variety of habitats; the only basic requirement seems to be association with permanent or semipermanent bodies of water. These habitats include such diverse situations as sandy beach, salt marsh, roadside ditch, pine flatwoods, grassy stream bank, marshy meadow, rocky woodlands, sphagnum bog, and tamarack swamp. I have personally collected <u>T. sauritus</u> in most of these habitats; the other records are either from the literature or from field notes supplied by colleagues. Frequent reference has been made to the

semiarboreal tendencies of this species, which, by virtue of its relatively longer tail, is perhaps better adapted for such activity than is T. proximus. Carpenter (1952a) reports that 61 percent of the sauritus collected during the summer months were up in bushes.

Food

The diet of the eastern ribbonsnake consists chiefly of adult and larval amphibians, and fishes. Species definitely known to have been eaten by Thamnophis sauritus under natural conditions are listed in Table 13. Several authors (Surface, 1906; Carpenter, 1952a; Hamilton and Pollack, 1956) have found invertebrates in the stomach contents of ribbonsnakes, and Fowler (1937) terms sauritus as largely insectivorous. On the basis of present knowledge, Fowler's statement does not seem to be justified, and the few instances in which invertebrates actually have been found in sauritus are probably cases of secondary or accidental ingestion. The eastern ribbonsnake does not seem any more prone than its western counterpart to voluntarily eat invertebrates, lizards, or endothermic vertebrates.

Nocturnal prowling and feeding is an extremely common phenomenon in the species, especially in the southern part of the range and during the warm months of the year.

Table 13.--Food of Thamnophis sauritus

Species	Source
Anurans	
Bufo quercicus	Bullman and Schwartz, 1950
Bufo terrestris	Bullman and Schwartz, 1950
Acris gryllus	personal observation
Hyla cinerea	Bullman and Schwartz, 1950
Hyla crucifer	Carpenter, 1952a
Hyla gratiosa	Bullman and Schwartz, 1950
Hyla versicolor	Carpenter, 1952a
Pseudacris nigrita	Bullman and Schwartz, 1950
Pseudacris ocularis	Carpenter, 1952a
Rana areolata (larvae only)[a]	personal observation
Rana clamitans	Carpenter, 1952a
Rana palustris	Carpenter, 1952a
Rana pipiens	Carpenter, 1952a
Rana sylvatica	Carpenter, 1952a; Conant, 1951
Salamanders	
Leurolestes viridescens	Carpenter, 1952a
Ambystoma maculatum	Carpenter, 1952a
Pseudotriton ruber	Conant, 1951
Fishes	
Notemigonus chrysoleucas	Carpenter, 1952a
Gambusia affinis[a]	personal observation
Heterandria formosa[a]	personal observation

[a]Identified by Wm. M. Tolliver, Jr.

Reproduction

Carpenter (1953b) has found that female ribbonsnakes in southern Michigan attain sexual maturity at an age of between two and three years, and a minimum body length of 421 mm. Corresponding data for males are not presented. McCauley (1945) reports a gravid female from Maryland which is 344 mm. in body length. The seven smallest gravid female sauritus I have measured have body lengths of 332 (Pennsylvania), 346 (Georgia), 350 (West Virginia), 365 (Nova Scotia), 371 (Georgia), 374 (West Virginia), and 410 (Ohio) mm., respectively. Thamnophis sauritus apparently matures at a smaller body size than does T. proximus.

Mating apparently occurs in April in the northern part of the range where spring emergence takes place in the latter part of March; in the extreme southern portion of the range where there is no true winter hibernation, mating probably occurs earlier. The young are usually born in August in the North, July in the South, although there is much overlap. Dates range from 2 July through 4 October (personal observations). The latter date, surprisingly enough, is for a female from northern Florida, and there is a slight possibly that it might have been her second brood of the year. Tinkle (1957) has indicated that this phenomenon may have occurred in a female proximus from southeastern Louisiana. Telford (1952) reports that a female which gave birth to 14 normal young on 9 July bore

4 additional young on 16 September of the same year. The latter were malformed and born dead.

Brood size ranges from 3 (Hitmars, 1896) to 20 (Telford, 1954), the mean for 93 broods being 11 individuals. There appears to be pronounced geographic variation in brood size. The mean number of individuals is 15.8 in twelve broods from Florida, 14.9 in nine broods from southern Ontario, 10.7 in seven broods from Maryland (McCauley, 1945), 10.0 in five broods from southern Michigan (Carpenter, 1954a), and 6.0 in five broods from northern Michigan (Burt, 1928). The size of the brood tends to increase with the size of the female, hence these means may not be strictly comparable. Available data on body length of newly born T. sauritus are summarized in Table 14. Males average markedly larger than females in the southern part of the range, slightly, if at all larger, in the north. Young T. sauritus tend to average smaller at birth than T. proximus.

Burt (1928) has observed that there were twice as many embryos in the right oviduct as in the left one in the five female T. sauritus she examined, and Tinkle (1957) has found a similar relationship in 37 female T. proximus.

Parasites

Baumann (1909) reports an eastern ribbonsnake which was infected with haemosporidia.

TABLE 14.--Body length of newly born *Farancia abacura*

Locality	N	M	R
Alachua County, Florida[a]	3 ♂♂	170.7	144 -193
	6 ♀♀	155.7	137 -174
Broward County, Florida[a]	9 ♂♂	166.0	154.5-176
	7 ♀♀	160.4	157 -164.5
Collier County, Florida[a]	1 ♂	164.0	
	5 ♀♀	174.6	170.5-175
Nakulla County, Florida[a]	14 ♂♂	158.9	150 -164.5
	12 ♀♀	153.1	146.5-157.5
Sussex County, New Jersey[a]	3 ♂♂	153.0	144.5-147.5
	4 ♀♀	140.6	134.5-144.5
Trumbull County, Ohio[a]	13 ♂♂	154.4	146 -169
	7 ♀♀	150.0	138.5-165
Marshall County, Indiana[a]	3 ♂♂	141.0	125.5-146
	5 ♀♀	140.4	131.5-149.5
Washtenaw County, Michigan[a]	8 ♂♂	149.4	142 -157.5
	4 ♀♀	141.8	138 -145
Rondeau Provincial Park, Ontario[b]	12	150.1	150 -166
	11	164.9	153 -170
	9	149.9	144 -159
	21	149.3	142 -156
	9	141.1	130 -149
	13	154.4	142 -163
	9	165.3	160 -171
	11	154.2	140 -160
	15	163.7	149 -172

N = number of individuals; M = mean; R = range

[a]Personal observation
[b]Personal communication from B. Heyrick

Thamnophis sauritus is closely related to T. proximus and undoubtedly is derived from the latter species or its prototype. The reason for believing that the evolutionary sequence proceeded in this direction is that sauritus, with its longer tail and reduced number of supralabials, appears to be the more specialized form. Speciation may have occurred, as in many other species pairs (Blair, 1953), as the result of division during Pleistocene times into eastern and western populations which were confined during glacial periods in Floridian and Mexican refugia, respectively. To judge by the present distribution of the two species, it would appear that the Mississippi River (at a time when it was wider than at present) played an important role in the speciation process, probably by delaying the time when they again came in contact following the expansion of their ranges during the glacial retreat. When the two populations finally did come in contact, presumably first in southern Illinois, genetic isolation either was complete or nearly so. The great similarity between the two species in diet and habitat preference caused sufficient competition to prevent extensive sympatry. The overlap in ranges which does exist in

Indiana is probably the result of an eastward movement of proximus in the Prairie Peninsula during the Xerothermic period (see Smith, 1957); the populations in Indiana, and perhaps those in eastern Illinois and southeastern Wisconsin as well, represent relicts of that earlier, more eastward, distribution.

T. sauritus sackeni, except for its long, tail and small, separate parietal spots, bears a striking resemblance to T. proximus rutiloris of Gulf and Caribbean Middle America. The similarity is so great that some taxonomic confusion has revolved about a specimen of sackeni which bears incorrect locality data (see Wosmann, 1901). Two alternative hypotheses present themselves: either sackeni and rutiloris evolved independently in response to similar environmental conditions (which fails to take into account the montane populations of rutiloris), or sackeni was derived from rutiloris prior to the partition of the ribbonsnake into two species (sackeni in this case would be thought to resemble most closely the prototype of the species sauritus, and rutiloris the prototype of T. proximus). The constancy with which the presumably ancestral supralabial number (8) is maintained in sackeni would seem to indicate that it is the most primitive race of T. sauritus; the relatively short tail of T. s. septentrionalis is apparently a secondary modification. Deriving sackeni in this manner would serve to explain how,

other than through independent evolution, the species sauritus acquired the dark ventrolateral stripe present in Mexican and Central American T. proximus but lacking in those races which are in contact with T. sauritus at the present time.

The ranges of auduboni and vitticeps are now separated by over 1000 miles and the ranges of two other subspecies, i. e. sauritus and i. n. erythrus, but roughly comparable disjunctions occur between the Mexican and eastern United States subspecies of Pituophis, cornis and storeria occipitomaculata, although only in the latter instance has another race of the same subspecies been interposed between the pair which became separated (that is, if s. o. obscura of Florida is more closely related to s. o. texilineata of eastern Mexico than either are to the nominate race, as certain elements of color pattern seem to indicate). When the ribbonsnakes were able to expand their ranges, following the retreat of the glaciers, it was the derivatives rather than the original stock (or, being more accurate, the forms most nearly like the original stock) which moved northward and eastward (in the case of T. proximus), or northward and westward (T. sauritus).

The sauritus group is, ecologically speaking, both semiarboreal and semiaquatic. Its members have no peers within the genus in the former category, and in the latter must surely be considered the ecological equivalents in

eastern Mexico and eastern United States of Thamnophis sauritus, T. sirtalis, and the aquatic group of T. elegans of western North America. Several studies (Carpenter, 1954a; Fouquette, 1954) have compared the diet and habitat preference of the ribbonsnakes with those of the other species of Thamnophis with which they are sympatric, and have shown that the diets and habitat preferences of the several species are different enough that serious competition between them rarely arises. These studies indicate that of the sympatric species T. sirtalis is most like the ribbonsnakes in habitat preference, although not in diet.

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BIOGRAPHICAL SKETCH

Douglas Athon Rossman was born July 4, 1936, at Waukesha, Wisconsin. In June, 1954, he was graduated from Princeton High School, Princeton, New Jersey. In June, 1958, he received the degree of Bachelor of Arts from Southern Illinois University, Carbondale, with a major in zoology and minors in anthropology and botany. In September, 1958, he enrolled in the Graduate School of the University of Florida. He worked as a graduate assistant in the Department of Biology until June, 1959, and as a graduate fellow until June, 1961. From September, 1958, until the present time he has pursued his work toward the degree Doctor of Philosophy.

Douglas Athon Rossman is married to the former Nita Jane Kuster and will become the father of one child in August. He is a member of the Herpetologists' League, the American Society of Ichthyologists and Herpetologists, the Society of Systematic Zoologists, Phi Sigma Biological Society, and Phi Kappa Phi. He has published eleven technical papers in the fields of herpetology and protozoology.

This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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